Grass Vegetation:
An Indispensable Biotic Component of the Northern Mixed Grass Prairie

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Prairie ecosystems are complex; exceedingly more complex than the most complicated machines ever built by humans. The long-standing standard process to understand complex systems is to initially investigate the separate component parts. The gained knowledge of each part combined with the synergistic effects resulting when the parts work together provide the information needed to develop an understanding of the whole ecosystem. This classical concept of biological systems was developed by the Greek philosopher/scientist Aristotle (384-322 BC) who taught that "the whole is greater than the sum of its parts".

The goals of this study were developed by Dr. Warren C. Whitman (c. 1950) and Dr. Harold Goetz (1963) which were to gain quantitative knowledge of each component part and to provide a pathway essential for the understanding of the whole prairie ecosystem that would result in the development and establishment of scientific standards for proper management of native rangelands of the Northern Plains. The introduction to this study can be found in report DREC 16-1093 (Manske 2016).

Grass vegetation, rhizosphere organisms, and domesticated graminivores are indispensable biotic components of a functional rangeland ecosystem. Grazing graminivores depend on grass plants for nutritious forage. Grass plants depend on rhizosphere organisms for mineralization of essential elements from the soil organic matter. Rhizosphere organisms, which are achlorophyllous, depend on grass plants for short carbon chain energy that is exudated through the roots of lead tillers at vegetative growth stages following partial defoliation by grazing graminivores. Grass plants produce double the leaf biomass than is needed for photosynthesis in order to attract the vital partial defoliation by grazing graminivores on which they depend.

The three indispensable biotic components of rangeland ecosystems: Grass Vegetation, Rhizosphere Organisms, and Domesticated Graminivores will each be quantitatively described in separate companion reports. This report will provide quantitative knowledge of grass vegetation as an indispensable biotic component of grassland ecosystems.

Indispensable Grass Vegetation

Grass vegetation on a fully functional grassland ecosystem can be perpetually sustainable with biologically effective management that activates the ecosystem biogeochemical processes and the grass plant physiological mechanisms to function at potential levels. When these processes and mechanisms function above threshold levels, capture and replenishment of input essential elements occurs at greater quantities than the amount of output essential elements maintaining the ecosystem.

Grass Tiller Growth and Development

Grass plants use the major and minor essential elements in the inorganic form to synthesize vital organic compounds of carbohydrates, proteins, and nucleic acids for growth. Grass tillers consist of shoots and roots (figure 1). The shoot is the stem and leaves comprised of repeated phytomers (Beard 1973, Dahl 1995). A phytomer consists of a leaf, with a blade and a sheath separated by a collar, a node, an internode, and an axillary bud (Hyder 1974, Dahl and Hyder 1977). Each tiller shoot generally produces 6 to 8 phytomers per growing season (Langer 1972, Dahl 1995). Longevity of grass tillers extends two growing seasons (Langer 1956, Butler and Briske 1988, Manske 2009, 2014a). Phytomers develop from leaf primordia that form on alternating sides of the apical meristem (Evans and Grover 1940, Langer 1972, Beard 1973, Dahl 1995). Almost all of the phytomer cells are produced in the apical meristem while the leaf primordia is a minute bud (Langer 1972). Growth of the leaf results through cell enlargement and elongation (Esau 1960, Dahl 1995). Once a leaf blade is fully expanded, it has its greatest dry weight and no further growth of that blade is possible (Dahl 1995). Grass tillers remain vegetative during the first growing season, overwinter, and resume growth during the second subsequent growing season (Briske and Richards 1995). Production of new leaf primordia continues until the status of the apical meristem changes from vegetative to reproductive (Dahl 1995, Briske and Richards 1995). When the second year lead tiller is between the third new leaf stage and the three and a half new leaf stage, the apical meristem ceases to produce leaf primordia and begins to produce flower primordia (Frank 1996, Frank et al. 1997). The flower bud primordia develop into the inflorescence with the apical dome becoming the terminal spikelet (Langer 1972). Previously formed leaf buds continue to grow and develop (Esau 1960, Langer 1972) until the flower stalk elongates (Dahl 1995). The life cycle of a grass tiller terminates during the end of the second growing season because production of additional leaves is no longer possible (Briske and Richards 1995).

Grass Plant Mechanisms

The key factor in meeting grass plant biological requirements is proper timing of partial defoliation. The effects of defoliation are not simply the removal of herbage from grass plants (Langer 1963, 1972): foliage removal disrupts plant growth and photosynthesis, and defoliation also changes physiological mechanisms in all parts of the plant; alters the plant community microclimate by changing light transmission, moisture relations, and temperature (Briske and Richards 1994, 1995); and changes the soil environment, thereby affecting soil organism activity and ecosystem biogeochemical processes (Manske 2000a, 2011a). Internal plant mechanisms help grass tillers withstand and recover from partial defoliation by grazing. The primary mechanisms are: compensatory physiological mechanisms (McNaughton 1979, 1983; Briske 1991); vegetative reproduction by tillering (Mueller and Richards 1986, Richards et al. 1988, Murphy and Briske 1992, Briske and Richards 1994, 1995); nutrient resource uptake (Crider 1955, Li and Wilson 1998, Kochy and Wilson 2000, Peltzer and Kochy 2001); and water use efficiency (Wight and Black 1972, 1979).

Compensatory Physiological Mechanisms

The compensatory physiological mechanisms give grass plants the capability to replace lost leaf and shoot biomass following grazing by increasing meristematic tissue activity, increasing photosynthetic capacity, and increasing allocation of carbon and nitrogen. Fully activated mechanisms can produce replacement foliage at 140% of the weight that was removed during grazing (Manske 2000b, 2010a, b, 2014a, b). The growth rates of replacement leaves and shoots increase after partial defoliation by grazing. The enhanced activity of meristematic tissue produces larger leaves with greater mass (Langer 1972, Briske and Richards 1995). Developing leaf primordia not fully expanded at time of defoliation have increased growth rates and tend to grow larger than leaves on undefoliated tillers (Langer 1972). Partial defoliated tillers increase photosynthetic rates of remaining mature leaves and rejuvenated portions of older leaves not completely senescent (Atkinson 1986, Briske and Richards 1995). Changes in cytokinin levels and other signals produced as a result of the increase in the root-shoot ratio rejuvenate the photosynthetic apparatus, inhibit or reduce the rate of senescence, and increase the lifespan and leaf mass of remaining mature leaves (Briske and Richards 1995). Activation of the compensatory physiological mechanisms after partial defoliation of grass tillers by grazing requires alternative sources of abundant carbon and nitrogen (Coyne et al. 1995). Carbon fixed during current photosynthesis in remaining mature leaf and shoot tissue and rejuvenated portions of older leaves is preferentially allocated to areas of active meristematic tissue (Ryle and Powell 1975, Richards and Caldwell 1985, Briske and Richards 1995, Coyne et al. 1995). The quantity of leaf area required to fix adequate quantities of carbon is 67% to 75% of the predefoliated leaf area (Manske 1999, 2011a, 2014c). Very little, if any, of the carbon and nitrogen stored in the root system is remobilized to support compensatory growth (Briske and Richards 1995). The mobilizable nitrogen pools in the shoot tissue are reduced following partial defoliation. This loss in nitrogen from the shoot increases preferential use of the quantities of mineral nitrogen available in the media around the roots (Millard et al. 1990, Ourry et al. 1990). This available soil mineral nitrogen has been converted from soil organic nitrogen by active rhizosphere organisms, absorbed through the roots, and moved to areas of active meristematic tissue.

Vegetative Reproduction by Tillering

Vegetative secondary tillers are shoots that develop on lead tillers from growth of axillary buds by the process of tillering (Dahl 1995) (figure 2). Meristematic activity in axillary buds and the subsequent development of vegetative tillers is regulated by auxin, a growth-inhibiting hormone produced in the apical meristem and young developing leaves (Briske and Richards 1995). Tiller growth from axillary buds is inhibited indirectly by auxin interference with the metabolic function of cytokinin, a growth hormone (Briske and Richards 1995). Partial defoliation of young leaf material at vegetative growth stages 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 secondary tillers (Murphy and Briske 1992, Briske and Richards 1994). If no defoliation occurs before the flower (anthesis) stage, the lead tiller continues to hormonally inhibit secondary tiller development from axillary buds. Production of the inhibitory hormone, auxin, declines gradationally as the lead tiller reaches the flower stage. The natural reduction of auxin in the lead tiller usually permits only one secondary tiller to develop. This developing secondary tiller produces auxin that hormonally suppress development of additional axillary buds (Briske and Richards 1995). Vegetative tiller growth is the dominant form of reproduction in semiarid and mesic grasslands (Belsky 1992, Chapman and Peat 1992, Briske and Richards 1995, Chapman 1996, Manske 1999) not sexual reproduction and the development of seedlings. Recruitment of new grass plants developed from seedlings is negligible in healthy grassland ecosystems. The frequency of true seedlings is extremely low in functioning grasslands, and establishment of seedlings occurs only during years with favorable moisture and temperature conditions (Wilson and Briske 1979, Briske and Richards 1995), in areas of reduced competition from vegetative tillers, and when resources are readily available to the growing seedling.

Nutrient Resource Uptake

Grass plant dominance within a grassland community is related to the plants competitiveness at nutrient and water resource uptake. Crider (1955) found that grass tillers with 50% or more of the aboveground leaf material removed reduce root growth, root respiration, and root nutrient absorption resulting in reduced functionality of these grass plants. Reduction of active root biomass caused diminishment of grass plant health and vigor (Whitman 1974) that resulted in a loss of resource uptake efficiency and a suppression of the competitiveness of grass plants to take up mineral nitrogen, essential elements, and soil water (Li and Wilson 1998, Kochy 1999, Kochy and Wilson 2000, Peltzer and Kochy 2001). The loss of active root length contributed to the reduction of rhizosphere biomass and the decline of ecosystem biogeochemical processes (Coleman et al. 1983, Klein et al. 1988). The nutrient resource uptake competitiveness of healthy grasses is able to suppress the expansion of shrubs and prevent successful establishment of grass, forb, and shrub seedlings into grasslands (Peltzer and Kochy 2001). The grass growth form has competitive advantages of nutrient uptake over the shrub growth form (Kochy and Wilson 2000). Grass aboveground biomass is primarily productive photosynthetic leaves resulting in a high resource uptake efficiency. Grasses are good competitors for belowground nutrient resources and superior competitors for mineral nitrogen because of a high root: shoot ratio and no woody stems to maintain. Shrubs have a great reduction in resource uptake efficiency because a large portion of the photosynthates produced in the leaves must be used to build and maintain their unproductive woody stems. However, the taller woody stems make shrubs superior competitor for aboveground sunlight resources (Kochy and Wilson 2000). Competition for belowground nutrient resources from healthy grasses reduce the growth rates of shrub rhizomes and cause high mortality rates of young suckers (Li and Wilson 1998). Shrubs can compete for some of the belowground resources only after the grass plants have been degraded by ineffective management. Following the reduction in grass plant resource uptake competitiveness, the belowground resources no longer consumed by the smaller, less vigorous degraded grasses, are taken up by the shrub plants resulting in proportional increases of biomass production (Kochy and Wilson 2000). With greater nutrient resources, shrub rhizome suckers are able to establish a faster growth rate and a higher survival rate (Li and Wilson 1998). The resulting greater shrub stem density increases the competition for the aboveground resources of light causing strong suppression of the grasses (Kochy and Wilson 2000). Traditionally, the observation of increasing woody shrubs and trees into degraded grasslands would have been explained as a result of fire suppression (Humphrey 1962, Stoddart, Smith, and Box 1975, Wright and Bailey 1982).

Water Use Efficiency

Grasslands of the Northern Plains managed with traditional practices are notorious for their inhibitory deficiency in available soil mineral nitrogen (Goetz et al. 1978) which has been determined to cause the observed low herbage production. Deficiencies in mineral nitrogen limit herbage production more often than water in temperate grasslands (Tilman 1990). The total herbage biomass production on grassland ecosystems has been shown to increase with increases in the quantity of available soil mineral nitrogen (Rogler and Lorenz 1957; Whitman 1957, 1963, 1976; Smika et al. 1965; Goetz 1969, 1975; Power and Alessi 1971; Lorenz and Rogler 1972; Taylor 1976; Wight and Black 1979). Greater quantities of available soil mineral nitrogen has been shown to also cause the soil water use efficiency to improve in grassland plants (Smika et al. 1965, Wight and Black 1972, Whitman 1976, 1978). Using a proxy method, Wight and Black (1972) found that precipitation (water) use efficiency of grass plants improved when soil mineral nitrogen was available at threshold quantities of 100 lbs/ac and greater. The inhibitory deficiencies of mineral nitrogen on grasslands that had less than 100 lbs/ac of available soil mineral nitrogen caused the weight of herbage production per inch of precipitation received to be reduced an average of 49.6% below the weight of herbage produced per inch of precipitation on the grassland ecosystems that had greater than 100 lbs/ac of mineral nitrogen and did not have mineral nitrogen deficiencies (Wight and Black 1979). The efficiency of water use in grass plants function at low levels when mineral nitrogen is deficient and function at high levels when mineral nitrogen is available at threshold quantities of 100 lbs/ac or greater. The level of water use efficiency determines the level of herbage biomass productivity on grasslands.

Manske (2010a, b) found that the threshold quantity of 100 lbs/ac of available mineral nitrogen was also critical for functionality of the vegetative reproduction and the compensatory physiological mechanisms. Both these mechanisms function at high potential levels on grasslands that have 100 lbs/ac or greater available soil mineral nitrogen and do not function or function at extremely low levels on grasslands that have mineral nitrogen deficiencies (Manske 2009, 2010a, b, c, 2011b).

Grass Nutrient Quality Related to Phenological Stages

The available nutritional quality of pregrazed lead tillers of native cool and warm season grasses is closely related to the phenological stages of growth and development, which are triggered primarily by the length of daylight (Roberts 1939, Dahl 1995). The length of daylight increases during the growing season between mid April and 21 June and then decreases. All native cool and warm season grasses have adequate levels of energy throughout the growing season.

Native cool season grasses start early leaf greenup of vegetative carryover tillers in mid April and grow slowly until early May, reaching 59% of the leaf growth in height by mid May with crude protein levels above 16%. Most cool season grasses reach the 3.5 new leaf stage around early June at 73% of the leaf growth in height, contain levels of crude protein above 15% during early to mid June, reach 94% of the leaf growth in height by late June, and 100% of the leaf growth height by late July. Most cool season grasses reach the flower stage before 21 June. After the flower stage, crude protein levels begin to decrease below 15%. During the seed development stage, flower stalks reach 94% of the growth in height by late June and crude protein levels remain above 9.6% until mid July. The growth in height reaches 100% by late July when seeds are maturing and being shed. As the lead tillers mature, the fiber content increases and percent crude protein, water, and digestibility decrease. During late July, crude protein levels drop below 8.0% and below 6.5% in late August (Whitman et al. 1951, Goetz 1963, Manske 2000c, 2008b). Crude protein levels of cool season secondary tillers increase above 9.6% during July and August to 13.2% in early September, decrease during September, and drop below 9.6% in early to mid October (Sedivec 1999, Manske 2008b). Phosphorus levels of lead tillers drop below 0.18% in late July, when plants reach the mature seed stage (Whitman et al. 1951, Manske 2008a).

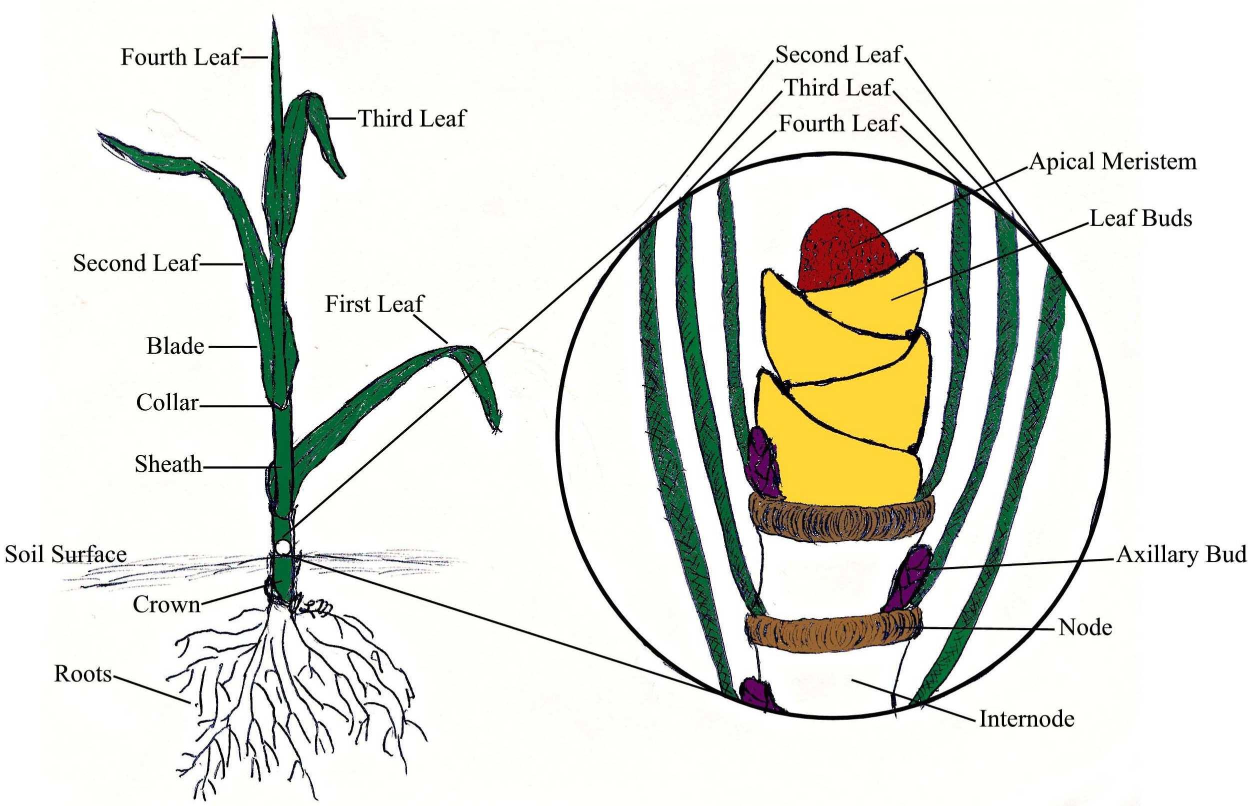
Native warm season grasses start early leaf greenup of vegetative carryover tillers in mid May, have crude protein levels above 15%, reach 44% of the leaf growth in height by early June, containing crude protein above 13% during early to mid June. Most warm season grasses reach the 3.5 new leaf stage around mid June, reaching 85% of the leaf growth in height by late June and reach 100% of height by late July. Seed stalks begin to develop in mid June and reach the flower stage after 21 June with 12.2% crude protein. During the seed development stage, crude protein levels remain above 9.6% until late July when the flower stalks reach 91% of the growth in height. As the lead tillers mature, the fiber content increases and percent crude protein, water, and digestibility decrease. During mid August, crude protein levels drop below 7.0%, seed stalks reach 100% of the growth in height by late August when the seeds are mature and being shed, and drop below 6.0% in crude protein by early September (Whitman et al. 1951, Goetz 1963, Manske 2000c, 2008b). Crude protein levels of warm season secondary tillers increase above 9.0% during August to 10.0% in early September, decreases during September, and drop below 9.6% in late September (Sedivec 1999, Manske 2008b). Phosphorus levels of lead tillers drop below 0.18% in late August, when plants reach the mature seed stage (Whitman et al. 1951, Manske 2008a).

Crude protein levels of upland sedges do not follow the same relationship with phenological growth stages as in cool and warm season grasses.

Crude protein levels in upland sedges remain high through the flower and seed mature stages. Upland sedges grow very early and produce seed heads in late April to early May and crude protein remains above 9.6% until mid July. Crude protein levels decrease with increases in senescence and drop below 7.8% in early August but do not fall below 6.2% for the remainder of the growing season (Whitman et al. 1951, Manske 2008b). Phosphorus levels drop below 0.18% in mid May when plants reach the mature seed stage (Whitman et al. 1951, Manske 2008a).

The quality of grass forage available to grazing graminivores on grasslands of the Northern Plains is above 9.6% crude protein in the lead tillers of the cool and warm season grasses during mid May to late July. Upland sedges have crude protein levels above 9.6% during early May to mid July. The secondary tillers of the cool and warm season grasses have crude protein levels above 9.6% during mid July to late September or mid October.

The early greenup of rangeland grass in the spring is not from new seedlings but from vegetative carryover tillers that did not produce a seedhead during the previous growing season. Spring growth of carryover tillers depends both on carbohydrate reserves and on photosynthetic products from the portions of previous years leaves that overwintered without cell wall rupture and regreened with chlorophyll. Grass tiller growth and development depend, in part, on some carbohydrate reserves in early spring because the amount of photosynthetic product synthesized by the green carryover leaves and the first couple of early growing new leaves is insufficient to meet the total requirements for leaf growth (Coyne et al. 1995). Grass growth also requires that the tiller maintains adequate leaf area with a combination of carryover leaves and new leaves to provide photosynthetic product for growth of sequential new leaves. The total nonstructural carbohydrates of a grass tiller are at low levels following the huge reduction of reserves during the winter respiration period, and the carbohydrate reserves remaining in the roots and crowns are needed for both root growth and initial leaf growth during early spring. The low quantity of reserve carbohydrates are not adequate to supply the entire amount required to support root growth and also support leaf growth causing a reduction in active growth until sufficient leaf area is produced to provide the photosynthetic assimilates required for plant growth and other processes (Coyne et al. 1995). Removal of aboveground leaf material from grass tillers not yet at the three and a half new leaf stage deprives tillers of foliage needed for photosynthesis and increases the demand upon already low levels of carbohydrate reserves.



Grass Tiller at 3.5 Leaf Stage

Figure 1. Grass Tiller Structures.

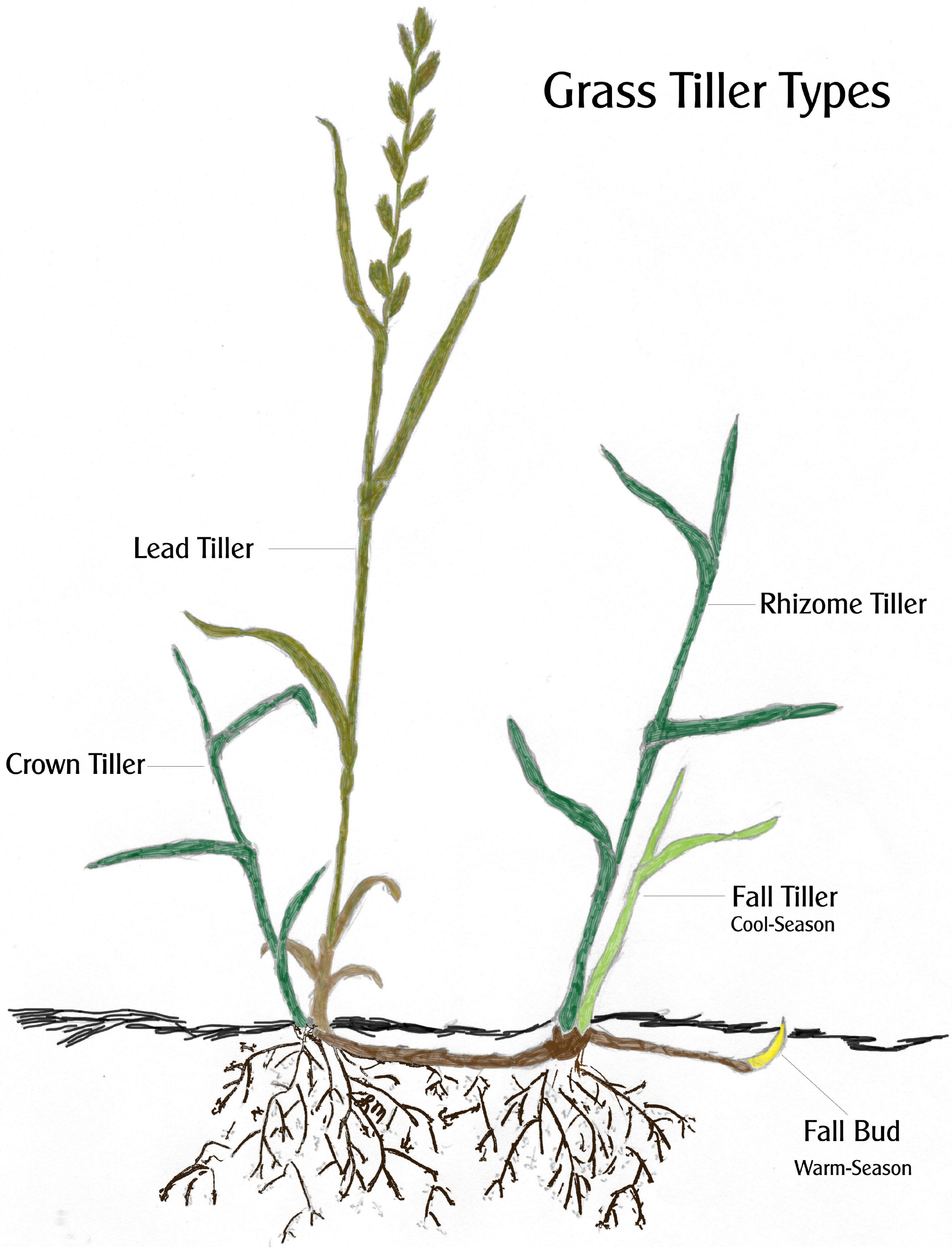


Figure 2. Vegetative Reproduction by Tillering.

1983-2012 Study of Grass Vegetation Weight Performance

Management Treatments

A 30 year study evaluated herbage weight performance during 6 monthly periods from May to October on native rangeland pastures managed by two distinctly different concepts. The traditional concept managed the land for its use as forage for livestock. The biologically effective concept managed the land as an ecosystem that considers the biological requirements of the grass plants, soil microbes, and the livestock.

Native Rangeland Pastures

The traditional concept was used to manage one native rangeland pasture (replicated two and three times during various periods) with a seasonlong system stocked with 7 cows/80 acres at 11.43 ac/AU and 2.60 ac/AUM for 4.5 months from 1 June to 15 October (137 days).

The biologically effective concept was used to manage three native rangeland pastures (replicated two times) with a twice-over rotation system stocked with 8 cows/80 acres at 10.22 ac/AU and 2.30 ac/AUM for 4.5 months from 1 June to 15 October (137 days).

Domesticated Graminivores

Commercial cow-calf pairs grazed the native rangeland pastures during this study. During 1983 to 1994, commercial Angus-Hereford cows with Charolais sired calves were used. These cows were assigned to separate herd pools for each grazing treatment. During 1995 to 2012, commercial crossbred cattle were used on all grazing treatments. Before spring turn out cow-calf pairs were sorted by cow age, and calf age with 50% steers and heifers.

Precipitation

The precipitation in inches and percent of long-term mean for perennial plant growing season months, April to October, and growing season months with water deficiency conditions are reported in the study introduction (Manske 2016). The 12 year period of 1983 to 1994 had a total of 72 growing season months, 31 months (43.1%) had water deficiency conditions, 14.5 months (20.1%) had high precipitation greater than 125% of LTM, and 26.5 months (36.8%) had normal precipitation greater than 75% and less than 125% of LTM. The 11 year period of 1995 to 2005 had a total of 66 growing season months, 15.5 months (23.4%) had water deficiency conditions, 27.5 months (41.7%) had high precipitation greater than 125% of LTM, and 23.0 months (34.8%) had normal precipitation greater than 75% and less than 125% of LTM. The 7 year period of 2006 to 2012 had a total of 42 growing season months, 13.5 months (32.1%) had water deficiency conditions, 11.0 months (26.2%) had high precipitation greater than 125% of LTM, and 17.5 months (41.7%) had normal precipitation greater than 75% and less than 125% of LTM.

Procedures

The effects on native rangeland grass vegetation from partial defoliation by grazing graminivores managed by the biologically effective concept was compared to that managed by the traditional concept. Changes in aboveground herbage biomass and % basal cover were evaluated with data collected during the growing season, May to October, from 1983 to 2012.

Aboveground herbage biomass was collected by the standard clipping method (Cook and Stubbendieck 1986). Vegetation on the grazed areas of each destructive sampling site was protected from grazing during one growing season by steel wire quonset type cages measuring 3 X 7 foot, which were moved to a new location each year prior to livestock turnout. The vegetation samples collected from the protective cages was labeled ungrazed during that growing season, however, the vegetation was grazed during all the years of the study except during the single year that the vegetation was protected from grazing by the placement of a cage. The herbage material from five 0.25 m^2 quadrats (frames) at each sample site from inside the cages (ungrazed) was hand clipped to ground level and sorted in the field by standard biotype categories: cool season, warm season, upland sedges, forbs, standing dead, and litter (the standing dead and litter categories were not included) only the living biomass was included in this report. The herbage of each biotype category from each frame was placed in labeled paper bags of known weight, oven dried at 140° F (60° C), and weighed. The mean monthly herbage biomass in lbs/ac for each biotype category of each year was replicated with n = 10 or 15 for the traditional concept and n = 15 or 30 for the biologically effective concept.

During May to August of the first four growing seasons of the study, the number of biotype categories were increased to only include one or two major plant species: Cool short (Prairie Junegrass and Plains reedgrass), Cool middle (Needle and Thread and Green needlegrass), Wheatgrass (Western and Thickspike wheatgrass), Warm short (Blue grama), Upland sedge (Threadleaf and Needleleaf sedges), and Forbs (all forbs). An additional category of Warm tall (Prairie sandreed) was collected on the sandy sites. Mean herbage biomass of biotype during the grazing period (June, July, and August) were determined. Herbage biomass data collected during September and October were placed in standard biotype categories. The data from the initial four years were further sorted into years 1-2 and years 3-4. The differences in herbage biomass production during these two 2 year periods should show the effects from the biologically effective management on the numerous biotype categories on the sandy, shallow, and silty ecological sites.

Plant species % basal cover was determined by the ten-pin point frame method (Cook and Stubbendieck 1986), with 2000 points collected along long-term transect lines outside (grazed) of each exclosure. Basal cover data of each plant species were sorted into standard biotype categories: cool season, warm season, and upland sedge. Basal cover for each biotype category of each year was replicated with n = 2 or 3 for the traditional concept and n = 3 or 6 for the biologically effective concept.

The evaluation of herbage biomass production and basal cover for graminoids on the biologically effective concept pastures compared to that on the traditional concept pastures during the entire 30 year study period, 1983 to 2012, used the standard biotype categories from the silty ecological sites.

Results

The traditional concept and the biologically effective concept were managed to have grazing periods that occurred at the same time, with the same number of days and number of months grazed.

The traditional concept for management of the seasonlong grazing strategy was developed to provide forage to grazing graminivores without consideration of the biological requirements of the grass plants and soil microbes, and did not consider the crude protein requirements of the cows. The single native rangeland pasture of the seasonlong system was grazed one time during the 4.5 month period from early June to mid October (137 days).

The biologically effective concept for management of the twice-over rotation grazing strategy was developed to coordinate partial defoliation events with grass phenological growth stages, meet the biological requirements of the grass plants and rhizosphere organisms, meet the nutritional requirements of the grazing graminivores, and enhance the ecosystem biogeochemical processes and activate the internal grass plant growth mechanisms to function at potential levels. Each of the three native rangeland pastures of the twice-over rotation system were grazed two times during the 4.5 month period from early June to mid October. The first grazing period of 15 days occurred between 1 June and 15 July, when grass lead tillers were between the three and a half new leaf stage and the flower stage. The second grazing period of 30 days occurred after 15 July and prior to mid October, when the stimulated vegetative secondary tillers had reached their three and a half new leaf stage. The first pasture grazed each year was the last pasture grazed the previous year. A three year sequence would be ABC, CAB, and BCA.

Initial four years, 1983-1986

The four year period of 1983 to 1986 had a total of 24 growing season months, 7.0 months (29.2%) had water deficiency conditions, 6.0 months (25.0%) had high precipitation greater than 125% of LTM, and 11.0 months (45.8%) had normal precipitation greater than 75% and less than 125% of LTM (Manske 2016).

During the first four years (1983-1986), herbage biomass data was collected with an increased number of biotype categories in order to follow the initial changes in the major grasses that resulted from the effects of the twice-over rotation strategy. Data for years 1-2 and years 3-4 for the sandy, shallow, and silty ecological sites are shown in tables 1, 2, and 3, respectively. The herbage biomass produced by the major grass and upland sedge species all had greatly increased during years 3-4 (tables 1, 2, and 3). The herbage biomass produced by the forb species decreased during years 3-4 (tables 1, 2, and 3).

Compared to the herbage biomass produced during years 1-2, the mean increase in herbage biomass produced on the sandy, shallow, and silty sites during years 3-4 was 196.93 lbs/ac for warm short, 121.92 lbs/ac for cool mid, 115.14 lbs/ac for upland sedge, 78.98 lbs/ac for cool short, 37.60 lbs/ac for wheatgrass, and 31.87 lbs/ac for warm tall, for a mean total increase of 582.44 lbs/ac for herbage biomass. The herbage biomass increase was 751.95

lbs/ac on the silty site, 545.68 lbs/ac on the sandy site, and 449.67 lbs/ac on the shallow site (tables 4, 5, and 6). A mean total loss of biomass was 37.00 lbs/ac for the forbs, the loss was 43.28 lbs/ac on the shallow site, 34.03 lbs/ac on the sandy site, and 33.69 lbs/ac on the silty site (tables 4, 5, and 6).

During years 3-4, the twice-over strategy increased herbage biomass production 32.5% for the grasses, 49.6% for the upland sedges, and decreased forb biomass 18.6% on the sandy site, increased herbage biomass production 65.7% for the grasses, 22.6% for the upland sedges, and decreased forb biomass 20.2% on the shallow site, and increased herbage biomass production 63.1% for the grasses, 64.7% for the upland sedges, and decreased forb biomass 13.2% on the silty site (tables 4, 5, and 6).

The total herbage biomass production was 31.5% greater on the sandy site, 40.1% greater on the shallow site, and 49.7% greater on the silty site during years 3-4 than the total production during years 1-2 (tables 4, 5, and 6).

Western wheatgrass and blue grama are both important grasses of the Northern Mixed Grass Prairie. Western wheatgrass is much taller than blue grama, however, blue grama usually has greater basal cover. Both grasses increase herbage biomass production when grazed using the twice-over treatment. During years 3-4, western wheatgrass increased biomass 71.9% and blue grama increased biomass 116.3%. Mean herbage biomass during June to August produced by western wheatgrass was 55.11, 37.27, and 212.10 lbs/ac on the sandy, shallow, and silty sites, respectively. Blue grama produced 184.48, 382.77, and 606.93 lbs/ac on the sandy, shallow, and silty sites, respectively. Blue grama outproduced western wheatgrass 234.8%, 927.0%, and 186.2% on the sandy, shallow, and silty sites, respectively (tables 1, 2, and 3, the separately collected wheatgrass data is with the cool middle grasses in table 1).

The great increase in herbage biomass for the grasses and upland sedges that occurred during years 3-4 on the sandy, shallow, and silty ecological sites was the result of belowground changes that started during years 1-2. Prior to 1983, the grassland was managed with seasonlong grazing. The biomass of the rhizosphere organisms was low and their low activity of mineralization of organic nitrogen had caused a deficiency in the availability of mineral nitrogen. The grass plant growth mechanisms: compensatory physiological mechanism, vegetative reproduction by tillering, nutrient resource uptake, and water use efficiency all require a minimum threshold level of 100 lbs/ac of available mineral nitrogen to function properly. The partial defoliation by the grazing graminivores that removed 25% to 33% of grass lead tillers at vegetative growth stages between the three and a half new leaf stage and the flower stage caused increased quantities of short chain carbon energy to be released from the tillers and exudated through the roots into the rhizosphere. The rhizosphere organisms are achlorophyllous and depend on short chain carbon energy from the grass plants at vegetative growth stages in quantities greater than the leakage rate. This process started building the rhizosphere microbe biomass during the first two years of the study. During the years 3-4, the rhizosphere biomass had increased to a sufficient quantity great enough to mineralize adequate quantities of mineral nitrogen that could support the functioning of the grass plant mechanisms. The grass plant growth mechanisms require activation which is also the partial defoliation by grazing graminivores that removed 25% to 33% of grass lead tillers at vegetative growth stages between the three and a half new leaf stage and the flower stage which occurs from 1 June to mid July each growing season. Activation plus an adequate supply of mineral nitrogen is required for the grass plant growth mechanisms to function. The combination of increasing the rhizosphere microbe biomass, the mineralization of adequate quantities of mineral nitrogen, and the activation of the grass plant growth mechanisms required two full growing seasons to show effects in aboveground herbage production resulting in the great increase in grass herbage biomass production during years 3-4. The reference rhizosphere weight of 406.44 kg/m^3 was measured during year 24. The maximum weight obtainable is still unknown. However, rhizosphere weights at slightly greater than 50% of the reference weight are able to mineralize 99.35 lbs/ac of mineral nitrogen. Rhizosphere weights at less than 50% of the reference weight are unable to mineralize adequate quantities of mineral nitrogen.

The increase in biomass of both endomycorrhizal fungi and ectomycorrhizal fungi greatly increase the amounts of secreted insoluble extracellular adhesive polysaccharides that form water-stable aggregates in the soil that are water permeable but not water soluble, and the increased soil aggregation improves soil quality, increases soil oxygenation, increases water infiltration, and increases water holding capacity (Harley and Smith 1983, Caesar-TonThat and Cochran 2000, Caesar-TonThat et al. 2001a, Caesar-TonThat et al. 2001b, Caesar-TonThat 2002, Manske and Caesar-TonThat

2003). Improvement of water infiltration and enlargement of the water holding capacity increases the effectiveness of the precipitation received, increases the quantity of soil water available for plant and soil microbe growth, and reduces plant growth problems between rain events. This improvement in soil quality is conducive to greater herbage biomass production.

Thirty years, 1983-2012

The 30 year period of 1983 to 2012 had a total of 180 growing season months, 60.0 months (33.3%) had water deficiency conditions, 53.0 months (29.4%) had high precipitation greater than 125% of LTM, and 67.0 months (37.2%) had normal precipitation greater than 75% and less than 125% of LTM (Manske 2016).

Thirty years, 1983 to 2012, of monthly herbage biomass and % basal cover data for standard biotype categories has been collected to evaluate effects on grass vegetation on the silty ecological sites from the biologically effective concept of management compared to the effects from the traditional concept of management. Thirty years of annual mean monthly herbage biomass (lbs/ac) by four standard biotype categories for the biologically effective concept (Appendix tables 1-4) and the traditional concept (Appendix tables 5-8) were summarized into 30 year means (tables 7 and 8 and figures 3 and 4).

The mean monthly herbage biomass values for the cool and warm season grasses on the biologically effective concept were greater than those on the traditional concept (tables 7 and 8 and figures 3 and 4). The mean monthly herbage biomass values for the upland sedges and forbs on the biologically effective concept were lower than those on the traditional concept, except the mean October upland sedge herbage weight was 10.66 lbs/ac greater on the biologically effective concept than that on the traditional concept (tables 7 and 8 and figures 3 and 4).

The cool season grasses on the biologically effective concept (table 7 and figure 3) produced a great lead tiller peak of 760.51 lbs/ac in July and then produced a greater secondary vegetative tiller peak of 826.89 lbs/ac in September. The secondary vegetative tillers were at growth stages greater than the three and a half new leaf stage and contained similar nutrient quality as the lead tillers had at the same growth stages. The cool season grasses on the traditional concept (table 8 and figure 4) produced a 20.3% lower lead tiller peak of 606.10 lbs/ac in July and than produced a 33.6% lower secondary vegetative tiller peak of 548.70 lbs/ac in September. The warm season grasses on the biologically effective concept (table 7 and figure 3) produced a lead tiller peak of 333.21 lbs/ac in August which is 16.1% greater than the lead tiller peak of 287.08 lbs/ac produced in August on the traditional concept (table 8 and figure 4).

The herbage biomass production of upland sedge on the silty site of the biologically effective concept increased 64.7% during years 3-4 compared to that during years 1-2 (table 6). After 30 years of treatment, the upland sedge herbage biomass on the biologically effective concept was produced at a 12.4% lower mean weight than that produced on the traditional concept (tables 9 and 10). The peak upland sedge biomass in July on the biologically effective concept was 204.99 lbs/ac (table 7 and figure 3) which was 13.8% lower than the peak upland sedge biomass in July at 237.83 lbs/ac on the traditional concept (table 8 and figure 4). During the initial stages after implementation of the biologically effective management concept, the upland sedge component greatly increased filling bare spaces in the plant community. The ecosystem continued to improve and develop. Around year 15, the cool and warm season grasses increased into the upland sedge areas and the upland sedges started to decrease.

The herbage biomass production of forbs on the silty site of the biologically effective concept decreased 13.2% during years 3-4 compared to that during years 1-2 (table 6). After 30 years of treatment, the forb herbage biomass on the biologically effective concept was produced at a 28.6% lower mean weight than that produced on the traditional concept (tables 9 and 10). The peak forb biomass in July on the biologically effective concept was 193.27 lbs/ac (table 7 and figure 3) which was 34.2% lower than the peak forb biomass in July at 293.73 lbs/ac on the traditional concept (table 8 and figure 4).

There is a huge biological advantage for grass plants to grow in an ecosystem that has the biogeochemical processes performed by the rhizosphere microbes functioning at potential levels and the four main grass plant growth mechanisms functioning with adequate quantities of available essential elements which are all made possible by the beneficial effects from the biologically effective twice-over rotation strategy. Greater quantities of live cool and warm season grasses are available during the entire grazing period from 1 June to 15

October. The cool season peak herbage biomass occurs in July. The peak on the traditional concept comes within 25.5% of the peak on the biologically effective concept which was the closest that the herbage weight on the two concepts came together (table 9). During June, the live cool season herbage biomass was 31.8% greater on the biologically effective concept. During August, September, and October, the live cool season herbage biomass was 36.5% greater on the biologically effective concept (table 9). The warm season peak herbage biomass occurs in August. The peak on the traditional concept came within 16.1% of the peak on the biologically effective concept which was the closest that the herbage weight on the two concepts came together (table 9). During June and July, the live warm season herbage was 31.1% greater on the biologically effective concept. During September and October, the live warm season herbage was 30.2% greater on the biologically effective concept (table 9).

During the period from mid July to mid October, traditionally managed pastures are usually deficient of adequate quantity and quality of grass forage. The mean July to October cool and warm season herbage biomass on the traditional concept was 802.05 lbs/ac. The mean July to October cool and warm season herbage biomass on the biologically effective concept was 1049.36 lbs/ac which provided 30.8% greater live grass forage containing abundant quantities of nutrients on the pastures managed by the biologically effective concept during the problem time period. This is the reason that cow and calf weight performance on the biologically effective concept is superior to that on the traditional concept.

The upland sedge peak herbage biomass occurs in July. The peak biomass on the biologically effective concept was 13.8% lower than the peak biomass on the traditional concept (table 9). During June, the upland sedge herbage biomass was 11.9% lower on the biologically effective concept than that on the traditional concept. During August, September, and October, the upland sedge herbage biomass was 13.7% lower on the biologically effective concept than that on the traditional concept (table 9).

The forb peak herbage biomass occurs in July. The peak biomass on the biologically effective concept was 34.2% lower than the peak biomass on the traditional concept (table 9). During June, the forb biomass was 32.9% lower on the biologically effective concept than that on the traditional concept. During August, September, and October, the forb herbage biomass was 24.7% lower on the biologically effective concept than that on the traditional concept (table 9).

Compared to the 30 year mean grass herbage biomass produced on the traditional concept, the grass herbage biomass produced on the biologically effective concept was 240.47 lbs/ac (31.2%) greater, the cool season biomass was 179.56 lbs/ac (33.3%) greater, and the warm season biomass was 60.91 lbs/ac (26.4%) greater (table 10). Compared to the 30 year mean grass percent basal cover produced on the traditional concept, the grass percent basal cover produced on the biologically effective concept was 8.36% (57.2%) greater, the cool season percent basal cover was 1.17% (20.0%) greater, and the warm season percent basal cover was 7.19% (82.1%) greater (table 11). On the biologically effective concept, the grass composition was 74.9% of the total live herbage biomass (table 10) and was 80.5% of the total basal cover (table 11). The composition of the cool season grass was 53.3% of the herbage biomass and 24.6% of the basal cover (tables 10 and 11). The composition of the warm season grass was 21.6% of the herbage biomass and 55.9% of the basal cover (tables 10 and 11).

Compared to the 30 year mean upland sedge herbage biomass and percent basal cover produced on the traditional concept, the upland sedge on the biologically effective concept had 24.0 lbs/ac (12.4%) lower herbage biomass and had 0.4% (6.7%) lower basal cover (tables 10 and 11). On the biologically effective concept, the upland sedge composition was 12.5% of the herbage biomass and 19.5% of the total basal cover (tables 10 and 11).

Compared to the 30 year mean forb herbage biomass produced on the traditional concept, the forbs on the biologically effective concept had 68.22 lbs/ac (28.6%) lower herbage biomass (table 10). On the biologically effective concept, the forb composition was 12.6% of the total herbage biomass (table 10).

Blue grama and upland sedges usually do not get credit for the ecological service they perform as protectors of the soil by reducing soil erosion, reducing soil temperature, reducing soil water evaporation, and reducing bare spots which reduces place for invasion of undesirable plants and pestiferous grasshoppers. On the tradition concept, blue grama and upland sedges have a basal cover of 14.7% with a composition of 71.6% (table 11). On the biologically effective concept, blue grama and upland sedge have a basal cover 46.3% greater at 21.5% with a composition of 75.4% (table 11). Both blue grama and upland sedges are extremely important plants in the Mixed Grass Prairie of the Northern Plains.

Vegetative Reproduction by Tillering

Increasing herbage biomass on grasslands requires full activation of the four primary internal plant mechanisms that help grass tillers withstand and recover from partial defoliation by grazing. The primary internal mechanisms are: compensatory physiological mechanisms (McNaughton 1979, 1983; Briske 1991); vegetative reproduction by tillering (Mueller and Richards 1986; Richards et al. 1988; Murphy and Briske 1992; Briske and Richards 1994, 1995); nutrient resource uptake (Crider 1955; Li and Wilson 1998; Kochy and Wilson 2000; Peltzer and Kochy 2001); and water use efficiency (Wight and Black 1972, 1979). The required initial step must be to raise the rhizosphere organism biomass to levels capable of mineralizing a threshold level of 100 lbs/ac (112/kg) or greater of available mineral nitrogen (Wight and Black 1972, 1979). Rhizosphere organisms are limited by accessing energy in the form of short carbon chains. Carbon energy can be released from grass lead tillers throught the roots into the rhizosphere by removal of 25% -33% of the aboveground leaf biomass by large grazing graminivores when the lead tillers are at the phenological growth stages between the three and a half new leaf stage and the flower (anthesis) stage during early June to mid July (Manske 1999, 2011b, 2014c). Full activation of internal grass plant mechanisms requires mineral nitrogen to be available at 100 lbs/ac (112 kg/ha) (Wight and Black 1972, 1979; Manske 2010 a,b). It also requires available carbon fixed through photosynthesis from 67% to 75% of the leaf area of predefoliated lead tillers before the flower stage (Manske 2010 a,b) and from 50% of the leaf area after the flower stage (Crider 1955). An increase in available mineral nitrogen and the other essential elements permits the grass tillers to synthesize increasing quantities of carbohydrates, proteins, and nucleic acids to accelerate growth rates of replacement leaves and shoots, increase photosynthetic capacity of remaining mature leaves, increase secondary tiller development from axillary buds, enhance the competitiveness of nutrient resource uptake, and improve water use efficiency. The combination of increased ecosystem biogeochemical processes and improved functioning of the internal grass plant mechanisms results in increases in grass herbage production and in plant density (basal cover) of the desirable grass species. Changes in the aboveground vegetation lag behind changes in the soil microorganism biomass and activity when a grassland ecosystem is degrading and also when it is aggrading.

Vegetative Tiller Study

Stimulation of vegetative reproduction of the grass tillering mechanisms is the primary factor needed to increase herbage biomass production on grasslands. Increasing the quantity and quality of grass herbage biomass by increasing grass tiller density is the key to improving livestock performance and increasing economic value captured per acre (hectare) from grasslands. The mechanisms of vegetative reproduction of secondary tillers from axillary buds are not a simple stimulus-response reaction. Activation of vegetative tillers can only occur at lead tiller vegetative phenological stages between the three and a half new leaf stage and the flower (anthesis) stage by partial defoliation by grazing graminivores that remove 25%-33% of aboveground leaf material with a minimum of a threshold quantity of 100 lbs/ac (112 kg/ha) of available mineral nitrogen and the quantity of available carbon fixed through photosynthesis from 67% to 75% of the predefoliated lead tiller leaf area. The quantity of herbage biomass is determined by grass tiller height and density. Grass tiller height is set by grass species genetics and the quantity of soil water. When grass leaf heights are similar, the management strategy that supports the greatest tiller density will produce the greatest quantity of herbage biomass.

A study that evaluated the differences in the quantity of secondary tillers produced vegetatively on the traditional seasonlong and the biologically effective twice-over rotation strategies with 25% leaf removal in mid June compared to a control of 0% leaf removal was conducted during the growing seasons of 2000 and 2001.

The grass tillers were classified by age and rate of growth. Lead tillers had rapid or unimpeded growth. Reproductive lead tillers developed into sexually reproductive stages. Vegetative lead tillers remained vegetative to the end of the growing season. Secondary tillers were initiated during the spring or summer and had inhibited growth rates regulated by a lead tiller. Secondary tillers could be held at the 2 or 3 leaf stage for long periods of time. Slow growth secondary tillers remained vegetative to the end of the growing season. Early senescent secondary tillers terminated growth prematurely before development of more than the 4 leaf stage during the growing season. Fall secondary tillers were cool season grass tillers initiated between mid August and mid October.

Carryover tillers maintained intact apical meristem, survived the winter period, and resumed growth and development the following growing season as lead tillers.

Procedures

The same grazing management treatments and cow-calf pairs of the 1983-2012 Study were used during the Vegetative Tiller Study. At the start of the vegetative tiller study, the grazing management strategies had continuous operation of 14 years for the traditional seasonlong and 17 years for the twice-over rotation system. Study site exclosures 16' X 32' (4.9 m X 9.8 m) made of stock panels were located on silty ecological sites on a gently sloping upland landscape with deep fine sandy loam soils. Seven randomly placed microplots composed each defoliation treatment. The microplots were PVC conduit barrier with a 3 inch (7.62 cm) diameter and 6 inch (15.24 cm) depth that were open at both end were inserted into the soil. Western wheatgrass was selected as the model species for vegetative tiller development. Every tiller within each microplot was identified with a different distinguishing loop of colored wire that encircled the tiller at its base. New tillers were identified by colored wire as they developed and carryover tillers were remarked at the start of the second year. The defoliation treatments included in this report are the control of 0% defoliation and mid June 25% defoliation treatments. The data collected biweekly for each tiller included number of leaves produced, phenological growth stage, and height of leaves. From these data determination of tiller density, tiller dynamics, tiller initiation, tiller termination, tiller growth and development, and dynamics of forage tiller density was possible.

Results

The two year period of 2000 to 2001 had a total of 12 growing season months, 3.5 months (29.2%) had water deficiency conditions, 3.5 months (29.2%) had high precipitation greater than 125% of LTM, and 5.0 months (41.7%) had normal precipitation greater than 75% and less than 125% of LTM (Manske 2016).

The entire vegetative tillering study included additional partial defoliation treatments that were detrimental to tiller growth. The treatments of mid May 25%, mid May 50%, and mid June 50% leaf removal resulted in substantially less tiller development than the tiller development on the control of 0% leaf removal.

Partial defoliation of mid May 25% and mid May 50% occurred before the tillers reached the three and a half new leaf stage and was extremely detrimental to tiller growth on all grazing management strategies. The combination of carryover leaf area and the remaining new leaf area after partial defoliation was insufficient to produce adequate quantities of nonstructural carbohydrates to support complete replacement of removed leaf area resulting in greatly reduced growth rates of herbage production with very few new tiller initiations during the growing season. The results from partial defoliation before the three and a half new leaf stage were similar to the results of previous partial defoliation treatments before the three and a half new leaf stage at Swift Current, Mandan, and Dickinson (table 12) (Campbell 1952, Rogler et al. 1962, Manske 2008c) and the reduced herbage production growth rates reported by Coyne et al. (1995).

Partial defoliation of mid June 50% occurred after the tillers had reached the three and a half new leaf stage but before the tillers had reached full leaf height development. The regreened carryover leaves had mostly senesced. The remaining new leaf area after partial defoliation of 50% was insufficient to produce adequate quantities of nonstructural carbohydrates to support complete replacement of removed leaf area on all grazing management strategies. The seasonlong management strategy had a low volume of rhizosphere microbes that mineralized nitrogen at below threshold levels of 112 kg/ha (100 lbs/ac) resulting in extremely low secondary tiller initiation (table 13). The twice-over management strategy had a high volume of rhizosphere microbes that mineralized nitrogen at levels greater than the threshold level of 112 kg/ha resulting in secondary tiller initiation similar to that of the control with 0% leaf removal (table 13). This reduction in secondary tiller development was caused by inadequate leaf area to fix the needed quantity of carbon. The remaining leaf area during the lead tiller vegetative stages between the three and a half new leaf stage and the flower stage needs to be between 67% to 75% of the predefoliated lead tiller leaf area. The amount of leaf area that can be removed is 25% to 33%. At this level, the partial defoliation removes sufficient quantities of auxin and stimulates the vegetative tillering mechanisms while retaining adequate quantities of new leaf area than can fix sufficient quantities of nonstructural carbohydrates to support complete replacement of removed leaf area and also support growth and development of the activated secondary tillers from axillary buds.

Tiller Density

Control Treatment

A total of 845.8/m^2 different tillers were present on the control treatment of the traditional seasonlong management strategy during two growing seasons (table 14), of which 188.0/m^2 were carryover tillers the first year and 657.8/m^2 were new initiated vegetative tillers. A total of 250.6/m^2 vegetative tillers terminated prematurely and 125.3/m^2 lead tillers terminated after flowering, resulting in 469.9/m^2 tillers remaining mid October at the end of the second growing season.

A total of 2098.8/m^2 different tillers were present on the control treatment of the twice-over management strategy during two growing seasons (table 14), of which 626.5/m^2 were carryover tillers the first year and 1472.3/m^2 were new initiated vegetative tillers. A total of 720.4/m^2 vegetative tillers terminated prematurely and 720.5/m^2 lead tillers terminated after flowering, resulting in 657.9/m^2 tillers remaining mid October at the end of second growing season.

Mid June 25% Treatment

A total of 908.5/m^2 different tillers were present on the mid June 25% defoliation treatment of the traditional seasonlong management strategy during two growing seasons (table 14), of which 250.6/m^2 were carryover tillers the first year and 657.9/m^2 were new initiated vegetative tillers. A total of 313.3/m^2 vegetative tillers terminated prematurely and 219.3/m^2 lead tillers terminated after flowering, resulting in 375.9/m^2 tillers remaining mid October at the end of the second growing season.

A total of 2255.6/m^2 different tillers were present on the mid June 25% defoliation treatment of the twice-over management strategy during two growing seasons (table 14), of which 595.2/m^2 were carryover tillers the first year and 1660.4/m^2 were new initiated vegetative tillers. A total of 877.2/m^2 vegetative tillers terminated prematurely and 344.6/m^2 lead tillers terminated after flowering, resulting in 1033.8/m^2 tillers remaining mid October at the end of second growing season.

The mid June 25% treatment of the seasonlong management strategy had 7.4% more total different tillers, 0.0% more initiated tillers, 41.7% more terminated tillers, and 20.0% fewer remaining tillers than that on the control treatment of the seasonlong management strategy (table 14). The mid June 25% treatment of the twice-over management strategy had 7.5% more total different tillers, 12.8% more initiated tillers, 15.2% fewer terminated tillers, and 57.1% more remaining tiller than that on the control treatments of the twice-over management strategy (table 14).

The control treatment of the twice-over management strategy had 148.1% more total different tillers, 123.8% more initiated tillers, 283.3% more terminated tillers, and 40.0% more remaining tillers than that on the control treatment of the seasonlong management strategy (table 14). The mid June 25% treatment of the twice-over management strategy had 148.3% more total different tillers, 152.4% more initiated tillers, 129.4% more terminated tillers, and 175.0% more remaining tillers than that on the mid June 25% treatment on the seasonlong management treatment (table 14).

Tiller Dynamics

Control Treatment

The first year on the control treatment of the traditional seasonlong management strategy (table 15, figure 5) 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. Assuming the lead 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 15, figure 5) 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 twice-over rotation management strategy (table 15, figure 5) 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. Assuming the lead 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 15, figure 5) 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 traditional seasonlong management strategy (table 15, figure 5) 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. Assuming the lead 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 15, figure 5) 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 twice-over rotation management strategy (table 15, figure 5) 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. Assuming the lead 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 15, figure 5) 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.

The mid June 25% treatment of the seasonlong management strategy had 55.6% greater pregrazed tiller density during the first May, 63.8% greater mean monthly tiller density during the first growing season, 15.4% lower pregrazed tiller density during the second May, and the same mean monthly tiller density during the second grazing season than that on the control treatment of the seasonlong management strategy (table 16, figure 5). The mid June 25% treatment of the twice-over management strategy had 10.7% greater pregrazed tiller density during the first May, 1.3% greater mean monthly tiller density during the first grazing season, 6.1% greater pregrazed tiller density during the second May, and 25.1% greater mean monthly tiller density during the second grazing season than that on the control treatment of the twice-over management strategy (table 16, figure 5).

The control treatment of the twice-over management strategy had 211.1% greater pregrazed tiller density during the first May, 231.9% greater mean monthly tiller density the first grazing season, 153.9% greater pregrazed tiller density during the second May, and 128.0% greater mean monthly tiller density during the second grazing season than that on the control treatment of the seasonlong management strategy (table 16, figure 5). The mid June 25% treatment of the twice-over management strategy had 121.4% greater pregrazed tiller density during the first May, 105.2% greater mean monthly tiller density during the first grazing season, 218.2% greater pregrazed tiller density during the second May, and 185.3% greater mean monthly tiller density during the second grazing season than that on the mid June 25% treatment of the seasonlong management strategy (table 16, figure 5).

Tiller Initiation

Control Treatment

A total of 657.9/m^2 secondary tillers were initiated by vegetative reproduction from axillary buds on the control treatment of the traditional seasonlong management strategy with 47.6% occurring during the spring, 14.3% occurring during the summer, and 38.1% occurring during the fall periods (table 17).

A total of 1472.3/m^2 secondary tillers were initiated by vegetative reproduction from axillary buds on the control treatment of the twice-over management strategy with 59.6% occurring during the spring, 10.6% occurring during the summer, and 29.8% occurring during the fall periods (table 17).

Mid June 25% Treatment

A total of 657.9/m^2 secondary tillers were initiated by vegetative reproduction from axillary buds on the mid June 25% defoliation treatment of the traditional seasonlong management strategy with 38.1% occurring during the spring, 23.8% occurring during the summer, and 38.1% occurring during the fall periods (table 17).

A total of 1660.4/m^2 secondary tillers were initiated by vegetative reproduction from axillary buds on the mid June 25% defoliation treatment of the twice-over management strategy with 62.3% occurring during the spring, 3.8% occurring during the summer, and 34.0% occurring during the fall periods (table 17).

The initiation of vegetative tillers during spring before grazing started appear to be more affected by the management and conditions of the previous growing season than to those of the current growing season. The initiation of vegetative tillers during the mid summer period had the lowest tiller numbers on all treatments of all management strategies because this period occurred simultaneously with the high resource demand period in which the dominant reproductive lead tillers progressed through the flower stages and produced seeds with low resources available for secondary tiller development. The cool season grass 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.

The mid June 25% treatment of the seasonlong management strategy had 20% lower spring initiated tiller density, 66.6% greater summer initiated tiller density, and the same fall initiated tiller density resulting in the same total initiated vegetative tiller density than that on the control treatment of the seasonlong management strategy (table 17). The mid June 25% treatment of the twice-over management strategy had 17.9% greater spring initiated tiller density, 60.0% lower summer initiated tiller density, and 28.6% greater fall initiated tiller density resulting in 12.8% greater total initiated vegetative tiller density than that on the control treatment of the twice-over management strategy (table 17).

The control treatment of the twice-over management strategy had 180.0% greater spring initiated tiller density, 66.6% greater summer initiated tiller density, and 75.0% greater fall initiated tiller density resulting in 123.8% greater total initiated vegetative tiller density than that on the control treatment of the seasonlong management strategy (table 17). The mid June 25% treatment of the twice-over management strategy had 312.5% greater spring initiated tiller density, 60.0% lower summer initiated tiller density, and 125.0% greater fall initiated tiller density resulting in 152.4% greater total initiated vegetative tiller density than that on the mid June 25% treatment of the seasonlong management strategy (table 17). It is important to note that during the biweekly measurements of huge numbers of tillers during two growing seasons no seedlings were encountered on any treatment of all the management strategies.

Development of vegetative secondary tillers from axillary buds is regulated by a growth inhibiting hormone, auxin, produced in the apical meristem and young developing leaves of lead tillers (Briske and Richards 1995). Auxin interferes with the performance of a growth hormone, cytokinin, preventing tiller growth from axillary buds. Partial defoliation that removes 25% to 33% of the leaf area of lead tillers at vegetative phenological growth between the three and a half new leaf stage and the flower stage reduces the quantity of lead tiller auxin permitting cytokinin to stimulate metabolic activity in the axillary buds. Secondary tiller growth and development from axillary buds also requires the availability of sufficient carbohydrates and essential elements. If these requirements are available, tiller initiation occurs soon after stimulation. However, if these requirements are not available, tiller initiation is delayed until sufficient nutrients become available. Some stimulated axillary buds may terminate at the end of the growing season from lack of adequate resources. Increasing grass tiller density in a grassland ecosystem requires management that intentionally stimulates axillary bud metabolic activity, retains 66% to 75% of the predefoliated tiller leaf area that can fix the required quantity of carbohydrates, and maintains a large enough rhizosphere microbial biomass to mineralize adequate amounts of essential elements.

Tiller Termination

Control Treatment

A total of 375.9/m^2 tillers terminated on the control treatment of the seasonlong management strategy (table 18), of which 250.6/m^2 were vegetative tillers terminated prematurely with 0.0% terminating during spring and 100.0% terminating during the grazing period, 125.3/m^2 were lead tillers terminated after flowering, and no tillers terminated during the winter period. A total of 469.9/m^2 remained alive resulting in a 44.4% termination rate.

A total of 1440.9/m^2 tillers terminated on the control treatment of the twice-over management strategy (table 18), of which 689.1/m^2 were vegetative tillers terminated prematurely with 40.9% terminating during spring and 59.1% terminated during the grazing period, 720.5/m^2 were lead tillers terminated after flowering, and 31.3/m^2 tillers terminated during the winter period. A total of 657.7/m^2 tillers remained alive resulting in a 68.7% termination rate.

Mid June 25% Treatment

A total of 532.6/m^2 tillers terminated on the mid June 25% defoliation treatment of the seasonlong management strategy (table 18), of which 313.3/m^2 were vegetative tillers terminated prematurely with 0.0% terminating during spring and 100.0% terminating during the grazing period, 219.3/m^2 were lead tillers terminated after flowering, and no tillers terminated during the winter period. A total of 375.9/m^2 tillers remained alive resulting in a 58.6% termination rate.

A total of 1221.8/m^2 tillers terminated on the mid June 25% defoliation treatment of the twice-over management strategy (table 18), of which 689.2/m^2 were vegetative tillers terminated prematurely with 18.2% terminating during spring and 81.8% terminating during the grazing period, 344.6/m^2 were lead tillers terminated after flowering, and 188.0/m^2 tillers terminated during the winter period. A total of 1033.8/m^2 tillers remained alive resulting in a 54.2% termination rate.

Winter survival and spring regrowth of carryover tillers depend on having adequate carbohydrate reserves. The quantity of carbohydrates stored during the winter hardening process is closely related to the amount of active leaf material on each tiller. Tillers with abundant leaf area during late summer and early fall can store adequate quantities of carbohydrates to survive the winter and produce robust leaves the following spring. Winter dormancy in perennial grasses is not total inactivity, but reduced activity. The crown, portions of the root system, and some leaf tissue remain at low activity and maintain physiological processes throughout the winter by using stored carbohydrates. Cool season grasses continue leaf growth at slow rates during winter. Some tillers with low carbohydrates reserves do not survive until spring. The rate at which plants respire, or use, stored carbohydrates during winter is affected by the amount of insulation standing plant material and snow provide from the cold winter air temperatures. The greater the amount of insulation, the more slowly the plant draws on its carbohydrate reserves. With low amounts of insulation, very rapid respiration can occur and deplete carbohydrate reserves before spring, causing tiller death called "winter kill".

The carryover tillers that survive to spring depend on the low amounts of remaining carbohydrate reserves and on the photosynthetic products produced from the portions of previous years leaves that overwintered without cell wall rupture and regreened with chlorophyll. A little later in the spring dependence on photosynthetic product produced by new young leaves increases. The low quantity of reserve carbohydrates and photosynthetic product from carryover leaves may not be adequate to supply the entire amount required to support root growth and also support new leaf growth causing either a great reduction in active growth or a stoppage of growth resulting in spring tiller termination.

During the grazing period, secondary vegetative tillers are totally dependent on a lead tiller for access to carbohydrates and mineral nitrogen during early leaf stages through the 3 leaf stage and maybe for most of the 4 leaf stage. These subordinate secondary tiller have slow and inhibited growth development with some secondary tillers remaining at the 2 and 3 leaf stage for most of the growing season. During periods when the lead tiller is experiencing high resource demand, such as, progressing through the flower stages or post partial defoliation processes to accelerate replacement leaf and shoot growth and increasing photosynthetic capacity of remaining mature leaves diverts nutrient resources away from secondary tillers at levels that may result in tiller termination.

The mid June 25% treatment of the seasonlong management strategy had the same low spring terminated tiller density, 25.0% greater grazing period terminated tiller density, 75.0% greater terminated flowering tiller density, and the same low winter terminated tiller density resulting in 41.7% greater total terminated tiller density than that on the control treatment of the seasonlong management strategy (table 18). The mid June 25% treatment of the twice-over management strategy had 55.6% lower spring terminated tiller density, 38.5% greater grazing period terminated tiller density, 52.2% lower terminated flowering tiller density, and 500.0% greater winter terminated tiller density resulting in 15.2% lower total terminated tiller density than that on the control treatment of the twice-over management strategy (table 18).

The control treatment of the twice-over management strategy had 100.0% greater spring terminated tiller density, 62.5% greater grazing period terminated tiller density, 475.0% greater terminated flowering tiller density, and 100.0% greater winter terminated tiller density resulting in 283.3% greater total terminated tiller density than that on the control treatment of the seasonlong management strategy (table 18). The mid June 25% treatment of the twice-over management strategy had 100.0% greater spring terminated tiller density, 80.0% greater grazing period terminated tiller density, 57.1% greater terminated flowering tiller density, and 100.0% greater winter terminated tiller density resulting in 129.4% greater total terminated tiller density than that on the mid June 25% treatment of the seasonlong management strategy (table 18).

Tiller Type Rate of Growth

The tiller types were classified as reproductive lead tillers, vegetative lead tillers, and secondary vegetative tillers. 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 then the vegetative lead tillers. The subordinate tillers with slow or inhibited growth were the secondary tillers.

Almost all grass tillers grow and develop during two growing seasons. Reproductive lead tillers are derived from carryover tillers that were vegetative lead tillers during the previous growing season and following development of sexual reproductive seed stalks, these reproductive lead tillers will terminate at the end of the growing season. Vegetative lead tillers are derived from carryover tillers that were cool season fall tillers or late season developed vegetative tillers of the previous growing season and from spring initiated tillers that were stimulated during the previous growing season. These vegetative lead tillers can produce 6 to 10 leaves during the growing season depending on when they became independent tillers. Most of these vegetative lead tillers will carryover and become the reproductive lead tillers of the next growing season. Secondary vegetative tillers are derived from current season stimulated and initiated spring and summer tillers that remain dependent on a lead tiller until the 3.5 new leaf or 4 leaf stage. These secondary tillers can produce 6 to 8 leaves during the growing season depending on when they become independent tillers. The quantity of carbohydrates that these secondary tillers are able to store during the winter hardening period, mid August to mid October, determines their future development. Most of the secondary tillers will carryover and become the vegetative lead tillers of the next growing season, with a few robust secondary tillers becoming reproductive lead tillers. Some of the secondary tillers with few functional leaves will be able to store only low levels of carbohydrates and will terminate during the winter.

All of the vegetative tillers that did not produce a seed head move into winter as living tillers even though their green chlorophyll has faded and they appear similar in color to the tan of terminated reproductive lead tillers. The green colored leaves that appear soon after the snow melts are not new leaves, they are carryover last years leaves with cell walls that did not rupture. The new leaf growth of the carryover tillers will depend on the quantity of carryover leaf area that regreens early that next spring. Removal of the carryover leaves during late season and winter grazing greatly reduces the density of surviving tillers and the quantity of new leaf production.

The reproductive lead tillers had the fastest rate of growth and development. Usually 5 to 8 leaves had developed when reproductive lead tillers reached the flower (anthesis) stage and no additional leaves were produced during development of flower stalk stages. Reproductive lead tillers that produced flower stalks early in the flower period had 5 to 6 leaves and tillers that produced flower stalks late in the flower period had 7 or 8 leaves. The period with the greatest rate of flower stalk development occurred between early June and mid July. The rate of leaf development of the reproductive tillers was not different among the defoliation treatments of the grazing management strategies. The flower period started at the same time on all defoliation treatments of every grazing management strategy. First flowers (anthesis) appeared during early June, before 21 June, the summer solstice, the day with the longest daylight of nearly 16 hours. However, the length of the flower period differed among the grazing management strategies. The end of the flower period occurred in early July on the control and mid June 25% treatments of the seasonlong management strategy and in mid July on the mid June 25% treatment and in early August on the control treatment of the twice-over management strategy. The low quantity of available mineral nitrogen of less than 100 lbs/ac (112 kg/ha) contributed to the shorter flowering periods on the traditional seasonlong management strategy. The quantity of available mineral nitrogen at greater than 100 lbs/ac contributed to the longer flowering periods on the treatments of the twice-over management strategy.

The vegetative lead tillers had the second fastest rate of growth and development. The vegetative lead tillers developed 3.6 leaves in 3 months from the 3.0 leaf stage in early May to the 6.6 leaf stage in early August. The vegetative lead tillers were at the 4.0 leaf stage during early June. The period with the greatest rate of leaf development occurred between early June and early July. The greatest rate of leaf development occurred on the mid June 25% treatment of the twice-over management strategy. The lowest rate of leaf development occurred on the control treatment of the seasonlong management strategy. The rate of leaf stage development was not different among the reproductive lead tillers that had not produced flower stalks and the vegetative lead tillers on the same treatments of the grazing management strategies.

The secondary tillers that survive to the end of the growing season were subordinate to a lead tiller and had very slow rates of growth and development. Secondary tillers developed at an average rate of 0.4 leaves per month. During early July, secondary tillers were at the 3.0 leaf stage on the seasonlong management strategy and at the 3.5 leaf stage on the twice-over management strategy. Secondary tillers were totally dependent on a lead tiller for access to carbohydrates and mineral nitrogen during early leaf stages through the 3.0 leaf stage and had very slow rates of leaf development. After the reproductive lead tillers had completed the greatest amount of leaf development around mid July, several of the secondary tillers developed additional leaves at faster rates. With the full development of leaf 3 and some of leaf 4, secondary tillers seemed to transition into being independent.

Most of the growth in tillers leaf height and most of the development in tiller leaf stage by the reproductive and vegetative lead tillers occurred during May, June, and July. Goetz (1963) found that lead tillers completed 100% of the growth in tiller leaf height and cool season grass flower stalk height by the end of July. In warm season grasses, a small amount of flower stalk elongation occurs after late July (Manske 2000c). This rapid growth period corresponds with the period of greatest precipitation. The precipitation received during May, June, and July accounts for more than 50% of the annual precipitation of the Northern Mixed Grass Prairie (Manske et al. 2010d).

Tiller Type Density

Control Treatment

A total mean monthly tiller density of 342.0/m^2 was present on the control treatment of the traditional seasonlong management strategy (table 19), with 62.7/m^2 reproductive lead tillers, 146.2/m^2 vegetative lead tillers, and 133.1/m^2 secondary vegetative tillers.

A total mean monthly tiller density of 898.0/m^2 was present on the control treatment of the twice-over management strategy (table 19), with 352.5/m^2 reproductive lead tillers, 266.3/m^2 vegetative lead tillers, and 279.3/m^2 secondary vegetative tillers.

Mid June 25% Treatment

A total mean monthly tiller density of 415.1/m^2 was present on the mid June 25% treatment of the traditional seasonlong management strategy (table 19), with 99.2/m^2 reproductive lead tillers, 159.2/m^2 vegetative lead tillers, and 156.6/m^2 secondary vegetative tillers.

A total mean monthly tiller density of 1049.4/m^2 was present on the mid June 25% treatment of the twice-over management strategy (table 19), with 172.3/m^2 reproductive lead tillers, 543.0/m^2 vegetative lead tillers, and 334.2/m^2 secondary vegetative tillers.

The mid June 25% treatment of the seasonlong management strategy (table 19) had 21.4% more total tiller types, with 58.2% more reproductive lead tiller types, 8.9% more vegetative lead tiller types, and 17.7% more secondary tiller types than that on the control treatment of the seasonlong management strategy. The mid June 25% treatment of the twice-over management strategy (table 19) had 16.9% more total tiller types, with 51.1% less reproductive lead tiller types, 103.9% more vegetative lead tiller types, and 19.7% more secondary tiller types than that on the control treatment of the twice-over management strategy.

The control treatment of the twice-over management strategy (table 19) had 162.6% more total tiller types, with 462.2% more reproductive lead tiller types, 82.1% more vegetative lead tiller types, and 109.8% more secondary tiller types than that on the control treatment of the seasonlong management strategy. The mid June 25% treatment of the twice-over management strategy (table 19) had 152.8% more total tiller types, with 73.7% more reproductive lead tiller types, 241.1% more vegetative lead tiller types, and 113.4% more secondary tiller types than that on the mid June 25% treatment of the seasonlong management strategy.

Forage Tillers

Not all grass tillers present on a grassland ecosystem are forage tillers. Forage tillers are that portion of grass tillers that provide nourishment for livestock. The grass tillers that do not have sufficient quantity of leaf stage development or quality of nutrients are not forage tillers. Reproductive lead tillers derived from carryover tillers are forage tillers when between the 4 leaf stage and flower stage. Vegetative lead tillers derived from carryover tillers or from early spring initiated tillers are forage tillers when between the 4 leaf and 10 leaf stages. Secondary tillers derived from growing season initiated tillers are forage tillers after they develop the 4 leaf stage until the 8 leaf stage. The number of forage tillers produced during a growing season are greatly affected by the grazing management strategy.

Control Treatment

Forage tillers on the control treatment of the seasonlong management strategy were comprised of 18% reproductive lead tillers which are derived from carryover tillers. The density of reproductive lead tillers between the 4 leaf stage and the flower stage increased from 15.6/m^2 in early May to 47.0/m^2 at start of grazing in early June as tillers developed additional leaves, then decreased to 15.6/m^2 in early July and 0.0/m^2 in mid July as lead tillers reached the flower stage (table 20, figure 6). Forage tillers were comprised of 43% vegetative lead tillers which are derived from carryover tillers and spring initiated tillers. The density of vegetative lead tillers between the 4 leaf stage and the 10 leaf stage increased from 15.6/m^2 in early May to 78.3/m^2 at start of grazing in early June, continued increasing to 156.6/m^2 in early July and remained at 156.6/m^2 until end of grazing in mid October (table 20, figure 6). Forage tillers were comprised of 39% secondary tillers which are derived from growing season initiated tillers. The density of secondary tillers between the 4 leaf stage and the 8 leaf stage remained at 0.0/m^2 from early May through early June, then increased to 15.6/m^2 in mid June, increased to 31.3/m^2 in mid July, decreased to 15.6/m^2 in early August, and increased to 47.0/m^2 in late August, and to 78.3/m^2 at end of grazing in mid October (table 20, figure 6). Density of mean total tillers was 341.5/m^2 during the grazing season. The density of total forage tillers between the 4 leaf stage and the flower stage or the 10 leaf stage started at 31.3/m^2 in early May, increased to 125.3/m^2 at start of grazing in early June, increased to 188.0/m^2 in early and mid July decreased to 172.3/m^2 in early August, increased to 203.6/m^2 in late August, and peaked at 235.0/m^2 at end of grazing in mid October (table 20, figure 6).

Forage tillers on the control treatment of the twice-over management strategy were comprised of 39% reproductive lead tillers which are derived from carryover tillers. The density of reproductive lead tillers between the 4 leaf stage and the flower stage increased from 125.3/m^2 in early May to 281.9/m^2 at start of grazing in early June as tillers developed additional leaves, then decreased to 156.6/m^2 in early July, to 31.3/m^2 in early August, and then to 0.0/m^2 as lead tillers reached the flower stage (table 20, figure 6). Forage tillers were comprised of 30% vegetative lead tillers which are derived from carryover tillers and spring initiated tillers. The density of vegetative lead tillers between the 4 leaf stage and the 10 leaf stage increased from 47.0/m^2 in early May to 188.0/m^2 at start of grazing in early June, continued increasing and peaked at 266.3/m^2 during early and mid July, then decreased to 235.0/m^2 in early August and remained at that level until end of grazing in mid October (table 20, figure 6). Forage tillers were comprised of 31% secondary tillers which are derived from growing season initiated tillers. The density of secondary tillers between the 4 leaf stage and the 8 leaf stage started at 31.3/m^2 in early May, increased to 78.3/m^2 at start of grazing in early June, continued to increase at 109.6/m^2 in early July and peaked at 172.3/m^2 in early August, then decreased to 156.6/m^2 at end of grazing in mid October (table 20, figure 6). Density of mean total tillers was 883.4/m^2 during the grazing season. The density of total forage tillers between the 4 leaf stage and the flower stage or the 10 leaf stage started at 203.6/m^2 in early May, increased to 548.2/m^2 at start of grazing in early June, peaked at 595.2/m^2 in mid June, then decreased to 532.5/m^2 in early July, to 438.6/m^2 in early August, and to 391.6/m^2 at end of grazing in mid October (table 20, figure 6).

Mid June 25% Treatment

Forage tillers on the mid June 25% treatment of the seasonlong management strategy were comprised of 24% reproductive lead tillers which are derived from carryover tillers. The density of reproductive lead tillers between the 4 leaf stage and the flower stage increased from 15.6/m^2 in early May to a peak of 62.7/m^2 at start of grazing in early June as tillers developed additional leaves, then decreased to 47.0/m^2 in mid June, to 31.3/m^2 in early July, and to 0.0/m^2 in mid July as lead tillers reached the flower stage (table 20, figure 6). Forage tillers were comprised of 38% vegetative lead tillers which are derived from carryover tillers and spring initiated tillers. The density of vegetative lead tillers between the 4 leaf stage and the 10 leaf stage increased from 47.0/m^2 in early May to 141.0/m^2 at start of grazing in early June, then peaked at 156.6/m^2 in mid June remaining at that level until early August, and decreased to 125.3/m^2 at end of grazing in mid October (table 20, figure 6). Forage tillers were comprised of 38% secondary tillers which are derived from growing season initiated tillers. The density of secondary tillers between the 4 leaf stage and the 8 leaf stage remained a 0.0/m^2 from early May through mid June, increased to 31.3/m^2 in early July until early August, peaked at 109.6/m^2 in late August, and decreased to 94.0/m^2 at end of grazing in mid October (table 20, figure 6). Density of mean total tillers was 429.2/m^2 during the grazing season. The density of total forage tillers between the 4 leaf stage and the flower stage or the 10 leaf stage started at 62.7/m^2 in early May, increased to 203.6/m^2 at start of grazing in early June to mid June, increased to 219.3/m^2 in early July, decreased to 188.0/m^2 during mid July to early August, then peaked at 234.9/m^2 in late August, and decreased to 219.3/m^2 at end of grazing in mid October (table 20, figure 6).

Forage tillers on the mid June 25% treatment of the twice-over management strategy were comprised of 16% reproductive lead tillers which are derived from carryover tillers. The density of reproductive lead tillers between the 4 leaf stage and the flower stage increased from 78.3/m^2 in early May and peaked at 172.3/m^2 at start of grazing in early June as tillers developed additional leaves, then decreased to 141.0/m^2 in mid June, to 62.7/m^2 in early July, to 15.6/m^2 in mid July, and to 0.0/m^2 in early August as lead tillers reached the flower stage (table 20, figure 6). Forage tillers were comprised of 52% vegetative lead tillers which are derived from carryover tillers and spring initiated tillers. The density of vegetative lead tillers between the 4 leaf stage and the 10 leaf stage increased from 188.0/m^2 in early May, to 532.5/m^2 at start of grazing in early June, then peaked at 579.5/m^2 in mid June, decreased to 516.9/m^2 in early July until early August, then decreased to 485.6/m^2 in late August until end of grazing in mid October (table 20, figure 6). Forage tillers were comprised of 32% secondary tillers which are derived from growing season initiated tillers. The density of secondary tillers between the 4 leaf stage and the 8 leaf stage started at 15.6/m^2 in early May, reached the level of 15.6/m^2 again at start of grazing in early June, increased to a first peak of 203.6/m^2 in early July, decreased gradually to 141.0/m^2 in early August until late August, and then increased to a second peak of 203.6/m^2 at end of grazing in mid October (table 20, figure 6). Density of mean total tillers was 1030.7/m^2 during the grazing season. The density of total forage tillers between the 4 leaf stage and the flower stage or the 10 leaf stage started at 281.9/m^2 in early May, increased to 720.5/m^2 at start of grazing in early June, continued to increase to peak of 783.2/m^2 in early July, then gradually decreased to 689.2/m^2 in mid July, to 657.8/m^2 in early August, to 626.6/m^2 in late August, and increased to 689.2/m^2 at end of grazing in mid October (table 20, figure 6).

The primary period the reproductive lead tillers were forage tillers was from early June until mid July while at phenological growth stages between the 4 leaf stage and the flower stage. The primary period the vegetative lead tillers were forage tillers was from early June until mid October while at phenological growth stages between the 4 leaf stage and 10 leaf stage. The primary period the secondary tillers were forage tillers was from early July until mid October while at phenological growth stages between the 4 leaf stage and 8 leaf stage. The forage tillers are comprised primarily of preflower reproductive lead tillers and vegetative lead tillers during the first grazing period from early June to mid July. During the second grazing period from mid July to mid October, the forage tillers are comprised primarily of vegetative lead tillers and secondary tillers.

Forage tiller density on the control treatment of the seasonlong management strategy was 160.6/m^2 (45.6%) during the early June to mid July grazing period and was 199.7/m^2 (59.8%) during the mid July to mid October grazing period. Forage tiller density on the mid June 25% treatment of the seasonlong management strategy was 203.6/m^2 (48.1%) during the early June to mid July grazing period and was 207.6/m^2 (47.9%) during the mid July to mid October grazing period. The beneficial affects from the mid June 25% treatment on forage tiller density was a 26.8% increase during the early June to mid July grazing period and was a 4.0% increase during the mid July to mid October grazing period with a total forage tiller density of 208.1/m^2 (48.5%) during the early June to mid October grazing period that was 16.3% greater than the total forage tiller density of 179.0/m^2 (52.4%) on the control treatment of the seasonlong management strategy (table 21).

Forage tiller density on the control treatment of the twice-over management strategy was 532.5/m^2 (60.2%) during the early June to mid July grazing period and was 411.2/m^2 (46.6%) during the mid July to mid October grazing period. Forage tiller density on the mid June 25% treatment of the twice-over management strategy was 740.1/m^2 (68.5%) during the early June to mid July grazing period and was 665.7/m^2 (66.8%) during the mid July to mid October grazing period. The beneficial affects from the mid June 25% treatment on forage tiller density was a 39.0% increase during the early June to mid July grazing period and was a 61.9% increase during the mid July to mid October grazing period with a total forage tiller density of 704.9/m^2 (68.4%) during the early June to mid October grazing period that was 48.6% greater than the total forage tiller density of

474.4/m^2 (53.7%) on the control treatment of the twice-over management strategy (table 21).

The control treatment of the twice-over management strategy had a 165.0% greater forage tiller density during the early June to mid October grazing period with 231.6% greater forage tiller density during the early June to mid July grazing period and 105.9% greater forage tiller density during the mid July to mid October grazing period than that on the control treatment of the seasonlong management strategy (table 21). The mid June 25% treatment of the twice-over management strategy had a 238.7% greater forage tiller density during the early June to mid October grazing period with 263.5% greater forage tiller density during the early June to mid July grazing period and 220.7% greater forage tiller density during the mid July to mid October grazing period than that on the mid June 25% treatment of the seasonlong management strategy (table 21).

The not forage tiller density on the control treatment of the seasonlong management strategy was 191.9/m^2 (54.4%) during the early June to mid July grazing period and was 134.5/m^2 (40.2%) during the mid July to mid October grazing period. The not forage tiller density on the mid June 25% treatment of the seasonlong management strategy was 219.3/m^2 (51.9%) during the early June to mid July grazing period and was 225.7/m^2 (52.1%) during the mid July to mid October grazing period. The beneficial affects from the mid June 25% treatment on the not forage tiller density was a 14.3% increase during the early June to mid July grazing period and was a 67.8% increase during the mid July to mid October grazing period with a total not forage tiller density of 221.1/m^2 (51.5%) during the early June to mid October grazing period that was 36.1% greater than the total not forage tiller density of 162.5/m^2 (47.6%) on the control treatment of the seasonlong management strategy (table 21).

The not forage tiller density on the control treatment of the twice-over management strategy was 352.5/m^2 (39.8%) during the early June to mid July grazing period and was 471.2/m^2 (53.4%) during the mid July to mid October grazing period. The not forage tiller density on the mid June 25% treatment of the twice-over management strategy was 340.7/m^2 (31.5%) during the early June to mid July grazing period and was 331.5/m^2 (33.2%) during the mid July to mid October grazing period. The beneficial affects from the mid June 25% treatment on the not forage tiller density was a 3.3% decrease during the early June to mid July grazing period and was a 29.6% decrease during the mid July to mid October grazing period with a total not forage tiller density of 325.8/m^2 (31.6%) during the early June to mid October grazing period that was a 20.3% decrease from the total not forage tiller density of 409.0/m^2 (46.3%) on the control treatment of the twice-over management strategy (table 21).

The control treatment of the twice-over management strategy had 151.7% greater not forage tiller density during the early June to mid October grazing period with 83.7% greater not forage tiller density during the early June to mid July grazing period and 250.3% greater not forage tiller density during the mid July to mid October grazing period than that on the control treatment of the seasonlong management strategy (table 21). The mid June 25% treatment of the twice-over management strategy had a 47.4% greater not forage tiller density during the early June to mid October grazing period with 55.4% greater not forage tiller density during the early June to mid July grazing period and 46.9% greater not forage tiller density during the mid July to mid October grazing period than that on the mid June 25% treatment of the seasonlong management strategy (table 21).

During the total early June to mid October grazing period there was a 10.2% greater forage tiller density than not forage tiller density on the control treatment and there was a 6.2% greater not forage tiller density than forage tiller density on the mid June 25% treatment of the seasonlong management strategy (table 21).

During the total early June to mid October grazing period there was a 16.0% greater forage tiller density than not forage tiller density on the control treatment and there was a 116.34% greater forage tiller density than not forage tiller density on the mid June 25% treatment of the twice-over management strategy (table 21).

The difference between the tiller densities of the forage tillers and the not forage tillers was not very much on the control and mid June 25% treatments of the seasonlong management strategy and on the control treatemnt of the twice-over management strategy, however, the difference between the tiller densities of the forage tillers and the not forage tillers was huge on the mid June 25% treatment of the twice-over management strategy (table 21).

Tillers that remain vegetative and carryover into the following growing season are able to continue production of leaf primordia becoming that growing seasons lead tillers. While reproductive lead tillers are at vegetative stages between the 3 leaf stage and 3.5 leaf stage, the apical meristem ceases producing leaf primordia and commences producing flower primordia (Frank 1996, Frank et al. 1997). At the 3.5 leaf stage, all of the leaf primordia that will develop into leaves during the second growing season have been produced on the apical meristem of reproductive lead tillers. All previously produced leaf primordia continue to grow and develop. The flower stalk development can eventually be observed externally at the boot stage. Reproductive lead tillers terminate new leaf growth and development with the emergence of the flower stalk and elongation of 4 or 5 of the upper internodes with the attached leaf sheaths. As the flower stalk develops, the fiber content increases and the percent crude protein, percent water, and digestibility decrease. Shortly after the flower (anthesis) stage, crude protein levels drop below 9.6%, the minimum requirements for lactating cows (NRC 1996). Between the flower stage and the seed mature stage, crude protein levels decrease rapidly and drop below 7.8% by early August and drop below 6.2% in late August (Whitman et al. 1951, Manske 2008b). Reproductive lead tillers at phenological stages advanced of the flower stage yield minuscule quantities of forage because the crude protein content is below the nutrient requirements of lactating beef cattle.

Vegetative lead tillers and secondary tillers at leaf stages earlier than the 3.5 leaf stage had insufficient new leaf area without the additional photosynthetic leaf area from the carryover leaves to meet the required amounts of photosynthetic product for normal leaf growth and development. These early leaf stage tillers are not physiologically ready for partial defoliation and are not forage tillers until after they reach the 3.5 new leaf stage.

Vegetative lead tillers between the 4 leaf stage and the 6 or 8 leaf stage and sometimes to the 10 leaf stage, and secondary tillers between the 4 leaf stage and the 6 leaf stage and sometimes to the 8 leaf stage provide the primary source of forage tillers with crude protein quality at or above the nutrient requirements of lactating beef cows. The density of forage tillers between the 4 leaf stage and the 6 to 10 leaf stage directly affects the quantity of herbage biomass and the level of available crude protein. The quantity of crude protein captured per acre is directly related to the quantity of pounds of calf weight produced per acre and inversely related to the cost per pound of calf weight produced (Manske 2008d).

The substantially lower tiller densities on the traditional seasonlong management strategy were the result of a very low rhizosphere volume of only 1552.3 cm^3/m^3 with a low microbial biomass able to mineralize 85.9 kg/ha (76.7 lbs/ac) of mineral nitrogen which is below the threshold quantity of 112 kg/ha (100 lbs/ac). Partially defoliated tillers were unable to replace the quantity of leaf area removed and could only support the growth and development of a few secondary vegetative tillers from axillary buds at a density of 657.9/m^2. The native cool and warm season grasses on the seasonlong management strategy produced a mean monthly herbage biomass of 769.96 lbs/ac that had one peak at 850.55 lbs/ac in July (table 22, figure 7). Traditionally managed strategies usually are deficient of adequate quantity and quality of grass biomass during late season from mid July to mid October. The seasonlong management strategy had a native grass mean biomass of 785.89 lbs/ac (table 22, figure 7) during the second grazing period with a tiller density of 433.3/m^2 of which 47.9% were forage tillers (table 21) and most of the vegetative tillers with crude protein and phosphorus content below the requirements of lactating beef cows (tables 23 and 24, figures 8 and 9).

The biologically effective twice-over management strategy coordinated partial defoliation with grass phenological growth stages resulting in a large rhizosphere volume of 5212.9 cm^3/m^3 with a large microbial biomass able to mineralize 199.2 kg/ha (177.9 lbs/ac) of mineral nitrogen which is well above the threshold quantity of 112 kg/ha (100 lbs/ac). Partially defoliated tillers were able to replace the quantity of leaf area removed at a rate of 140% growth and were able to support the growth and development of initiated vegetative tillers from axillary buds at a density of 1660.4/m^2 (152.4% greater than that on the seasonlong management strategy). The native cool and warm season grasses on the twice-over management strategy produced a mean monthly herbage biomass of 1010.43 lbs/ac (31.2% greater than that on the seasonlong management strategy) that had one peak with lead tillers at 1064.94 lbs/ac in July and a greater second peak with vegetative tillers at 1127.75 lbs/ac in September (table 22, figure 7). Biologically effective management strategies usually have adequate quantity and quality of grass biomass during late season from mid July to mid October. The twice-over management strategy had native grass mean biomass of 1044.16 lbs/ac (32.9% greater than that on the seasonlong management strategy) (table 22, figure 7) during the second grazing period with a tiller density of 997.2/m^2 (130.1% greater than that on the seasonlong management strategy) of which 66.8% were forage tillers (table 21) and most of the vegetative and all of the secondary tillers with crude protein and phosphorus content above the requirements of lactating beef cows (tables 23 and 24, figures 8 and 9).

Grassland ecosystems managed by the biologically effective concept function at the biological potential levels. The ecosystem biogeochemical processes performed by the large volume rhizosphere with a large biomass of microbes mineralize large quantities of nitrogen and other essential elements. At the threshold quantity of 100 lbs/ac (112 kg/ha) available mineral nitrogen, the four primary internal plant growth mechanisms (compensatory physiological mechanisms, vegetative reproduction by tillering, nutrient resource uptake, and water use efficiency) perform at their greatest possible rates to help grass tillers withstand and fully recover from partial defoliation by grazing graminivores.

Discussion

Prairie ecosystems are more complex than the most complicated machines built by humans. Fortunately, grassland managers do not need to know how to build a prairie ecosystem to manage it properly. But, like the captain of a nuclear submarine or the pilot of a jumbo jet, grassland managers do need an understanding of how the major parts function in order to maintain everything working at potential level while they are in command. Unlike the captain or the pilot, who have access to a large technical work force, the grassland manager is often the entire technical crew. Most grassland managers identify themselves as livestock producers because thay have misinterpreted that their source of income originates from the sale of the livestock rather than from the land. The source of livestock weight is from renewable essential elements associated with the ecosystem that are recaptured by plants and soil microbes, recycled by soil microbes, and made available to the livestock through the renewed growth of forage grass plants. Grass plants require essential elements to grow. These critical ecosystem biogeochemical processes that mineralize essential elements do not work automatically and have not been included in traditional management concepts. This is the reason grassland ecosystems managed by traditional concepts produce around 50% of their potential, with a range from 30% to 70% of potential. The rhizosphere microbes perform the ecosystem biogeochemical processes (Manske 2015). The greater the biomass of rhizosphere microbes, the greater quantity of biogeochemical processes performed. The rhizosphere microbes are achlorophyllous and depend on grass plants for the source of short carbon chain energy. Grass plants can exudate short carbon chain energy into the rhizosphere during vegetative growth stages of lead tillers between the three and a half new leaf stage and the flower stage which happens each year between 1 June and 15 July following partial defoliation that removes 25% to 33% of the aboveground leaf biomass from 60% to 80% of the tillers by grazing graminivores. This partial defoliation also activates the grass plant growth mechanisms into functionality when 100 lbs/ac of mineral nitrogen is available. The compensatory physiological mechanisms give grass plants the capability to rapidly replace lost leaf and shoot biomass by increasing meristematic tissue activity, increasing photosynthetic capacity, and increasing allocation of carbon and nitrogen. The vegetative reproduction by tillering mechanisms develops secondary tillers from growth of axillary buds. The nutrient resource uptake mechanisms enhance the competitiveness of nutrient and water resource uptake which maintains grass plant dominance within a grassland community. The water use efficiency mechanisms increases the quantity of herbage biomass produced per inch of precipitation received by 50.4%. These grass plant growth mechanisms must be activated by grazing graminivores but will not function unless 100 lbs/ac of mineral nitrogen is available through mineralization of organic nitrogen by rhizosphere microbes.

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Table 1. Growing season (May to August) herbage biomass (lbs/ac) by biotype categories on the sandy ecological site of the Biologically Effective management concept of years 1-2 and years 3-4, 1983-1986.

Sandy Years 1-2	May	Jun	Jul	Aug	Jun-Aug Mean
Cool Short	170.97	89.90	96.93	88.16	91.66
Cool Middle	268.80	334.75	400.21	342.14	359.03
Warm Tall	205.31	464.24	482.87	392.88	446.66
Warm Short	59.76	45.40	114.78	101.59	87.26
Upland Sedge	533.42	523.76	494.47	347.88	455.37
Forbs	82.66	140.94	197.03	211.30	183.09
Grasses	704.84	934.29	1094.79	924.77	984.61
Graminoids	1238.26	1458.05	1589.26	1272.65	1439.98
Total	1320.92	1598.99	1786.29	1483.95	1623.07
Years 3-4	**May**	**Jun**	**Jul**	**Aug**	**Jun-Aug Mean**
Cool Short	96.63	146.29	111.40	124.09	127.26
Cool Middle	321.76	440.06	462.06	449.57	450.56
Warm Tall	152.58	510.82	517.36	598.63	542.27
Warm Short	86.28	136.38	224.39	192.67	184.48
Upland Sedge	717.76	674.35	625.59	743.33	681.09
Forbs	107.04	123.30	160.16	163.73	149.06
Grasses	657.25	1233.55	1315.21	1364.96	1304.57
Graminoids	1375.01	1907.90	1940.80	2108.29	1985.66
Total	1482.05	2031.20	2100.96	2272.02	2134.72

Table 2. Growing season (May to August) herbage biomass (lbs/ac) by biotype categories on the shallow ecological site of the Biologically Effective management concept of years 1-2 and years 3-4, 1983-1986.

Shallow Years 1-2	May	Jun	Jul	Aug	Jun-Aug Mean
Cool Short	137.96	186.13	162.94	177.21	175.43
Cool Middle	125.92	261.16	220.33	340.05	273.85
Wheatgrass	8.03	40.29	28.10	24.98	31.12
Warm Short	124.88	132.81	140.94	160.07	144.61
Upland Sedge	235.34	218.54	137.07	165.02	173.54
Forbs	90.98	171.86	334.20	137.57	214.54
Grasses	396.79	620.39	552.31	702.31	625.01
Graminoids	632.13	838.93	689.38	867.33	798.55
Total	723.11	1010.79	1023.58	1004.90	1013.09
Years 3-4	**May**	**Jun**	**Jul**	**Aug**	**Jun-Aug Mean**
Cool Short	154.61	348.87	233.51	195.45	259.28
Cool Middle	220.97	292.78	401.20	374.64	356.21
Wheatgrass	10.70	59.47	13.08	39.25	37.27
Warm Short	125.83	330.84	413.89	403.59	382.77
Upland Sedge	227.86	230.53	244.61	162.94	212.69
Forbs	107.44	167.30	169.68	176.80	171.26
Grasses	512.11	1031.96	1061.68	1012.93	1035.53
Graminoids	739.97	1262.49	1306.29	1175.87	1248.22
Total	847.41	1429.79	1475.97	1352.67	1419.48

Table 3. Growing season (May to August) herbage biomass (lbs/ac) by biotype categories on the silty ecological site of the Biologically Effective management concept of years 1-2 and years 3-4, 1983-1986.

Silty Years 1-2	May	Jun	Jul	Aug	Jun-Aug Mean
Cool Short	95.74	120.42	154.91	223.99	166.44
Cool Middle	127.56	525.88	431.33	268.79	408.67
Wheatgrass	154.91	142.72	156.40	114.18	137.77
Warm Short	281.87	248.28	376.03	430.24	351.52
Upland Sedge	142.72	114.97	138.46	120.13	124.52
Forbs	147.18	286.03	311.01	167.70	254.91
Grasses	660.08	1037.30	1118.67	1037.20	1064.40
Graminoids	802.80	1152.27	1257.13	1157.33	1188.92
Total	949.98	1438.30	1568.14	1325.03	1443.83
Years 3-4	**May**	**Jun**	**Jul**	**Aug**	**Jun-Aug Mean**
Cool Short	194.36	300.70	278.70	272.36	283.92
Cool Middle	472.96	532.23	589.72	776.64	632.86
Wheatgrass	107.44	201.20	190.29	244.81	212.10
Warm Short	292.82	566.62	661.27	592.89	606.93
Upland Sedge	201.15	212.30	237.77	165.12	205.06
Forbs	200.60	302.49	218.44	142.72	221.22
Grasses	1067.58	1600.75	1719.98	1886.70	1735.81
Graminoids	1268.73	1813.05	1957.75	2051.82	1940.87
Total	1469.33	2115.54	2176.19	2194.54	2162.09

Table 4. Mean grazing season (June to August) herbage biomass (lbs/ac) by biotype categories on the sandy ecological site of the Biologically Effective management concept comparing years 3-4 to years 1-2, 1985-1986 to 1983-1986.

	Years 3-4 Herbage Biomass Composition		Years 1-2 Herbage Biomass Composition		Difference
Sandy Site	lbs/ac	%	lbs/ac	%	%
Cool Short	127.26	6.0	91.66	5.6	38.8
Cool Middle	450.56	21.1	359.03	22.1	25.5
Warm Tall	542.27	25.4	446.66	27.5	21.4
Warm Short	184.48	8.6	87.26	5.4	111.4
Upland Sedge	681.09	31.9	455.37	28.1	49.6
Forbs	149.06	7.0	183.09	11.3	-18.6
Grasses	1304.57	61.1	984.61	60.7	32.5
Graminoids	1985.66	93.0	1439.98	88.7	37.9
Total	2134.72		1623.07		31.5

Table 5. Mean grazing season (June to August) herbage biomass (lbs/ac) by biotype categories on the shallow ecological site of the Biologically Effective management concept comparing years 3-4 to years 1-2, 1985-1986 to 1983-1986.

	Years 3-4 Herbage Biomass Composition		Years 1-2 Herbage Biomass Composition		Difference
Shallow Site	lbs/ac	%	lbs/ac	%	%
Cool Short	259.28	18.3	175.43	17.3	47.8
Cool Middle	356.21	25.1	273.85	27.0	30.1
Wheatgrass	37.27	2.6	31.12	3.1	19.8
Warm Short	382.77	27.0	144.61	14.3	164.7
Upland Sedge	212.69	15.0	173.54	17.1	22.6
Forbs	172.26	12.1	214.54	21.2	-20.2
Grasses	1035.53	73.0	625.01	61.7	65.7
Graminoids	1248.22	87.9	798.55	78.8	56.3
Total	1419.48		1013.09		40.1

Table 6. Mean grazing season (June to August) herbage biomass (lbs/ac) by biotype categories on the silty ecological site of the Biologically Effective management concept comparing years 3-4 to years 1-2, 1985-1986 to 1983-1986.

	Years 3-4 Herbage Biomass Composition		Years 1-2 Herbage Biomass Composition		Difference
Silty Site	lbs/ac	%	lbs/ac	%	%
Cool Short	283.92	13.1	166.44	11.5	70.6
Cool Middle	632.86	29.3	408.67	28.3	54.9
Wheatgrass	212.10	9.8	137.77	9.5	54.0
Warm Short	606.93	28.1	351.52	24.3	72.7
Upland Sedge	205.06	9.5	124.52	8.6	64.7
Forbs	221.22	10.2	254.91	17.7	-13.2
Grasses	1735.81	80.3	1064.40	73.7	63.1
Graminoids	1940.87	89.8	1188.92	82.3	63.2
Total	2162.09		1443.83		49.7

Table 7. Mean monthly herbage biomass (lbs/ac) by biotype categories on the silty ecological sites of the Biologically Effective concept, 1983-2012.

Silty Site	May	Jun	Jul	Aug	Sep	Oct
Cool Season	397.73	637.66	760.51	670.20	826.89	698.80
Warm Season	179.90	217.06	304.43	333.21	300.86	302.53
Upland Sedge	165.99	199.29	204.99	175.74	127.28	137.21
Forbs	145.26	146.55	193.27	187.79	164.72	159.88
Grasses	577.63	854.72	1064.94	1003.41	1127.75	1001.33
Graminoids	743.62	1054.01	1269.93	1179.15	1255.03	1138.54
Total	888.88	1200.56	1463.20	1366.94	1419.75	1298.42

Table 8. Mean monthly herbage biomass (lbs/ac) by biotype categories on the silty ecological sites of the Traditional concept, 1983-2012.

Silty Site	May	Jun	Jul	Aug	Sep	Oct
Cool Season	308.46	483.96	606.10	515.39	548.70	542.12
Warm Season	123.98	157.64	244.45	287.08	222.68	241.69
Upland Sedge	168.26	226.16	237.83	222.50	151.45	126.55
Forbs	166.47	218.24	293.73	253.01	212.18	216.13
Grasses	432.44	641.60	850.55	802.47	771.38	783.81
Graminoids	600.70	867.76	1088.38	1024.97	922.83	910.36
Total	767.17	1086.00	1382.11	1277.98	1135.01	1126.49

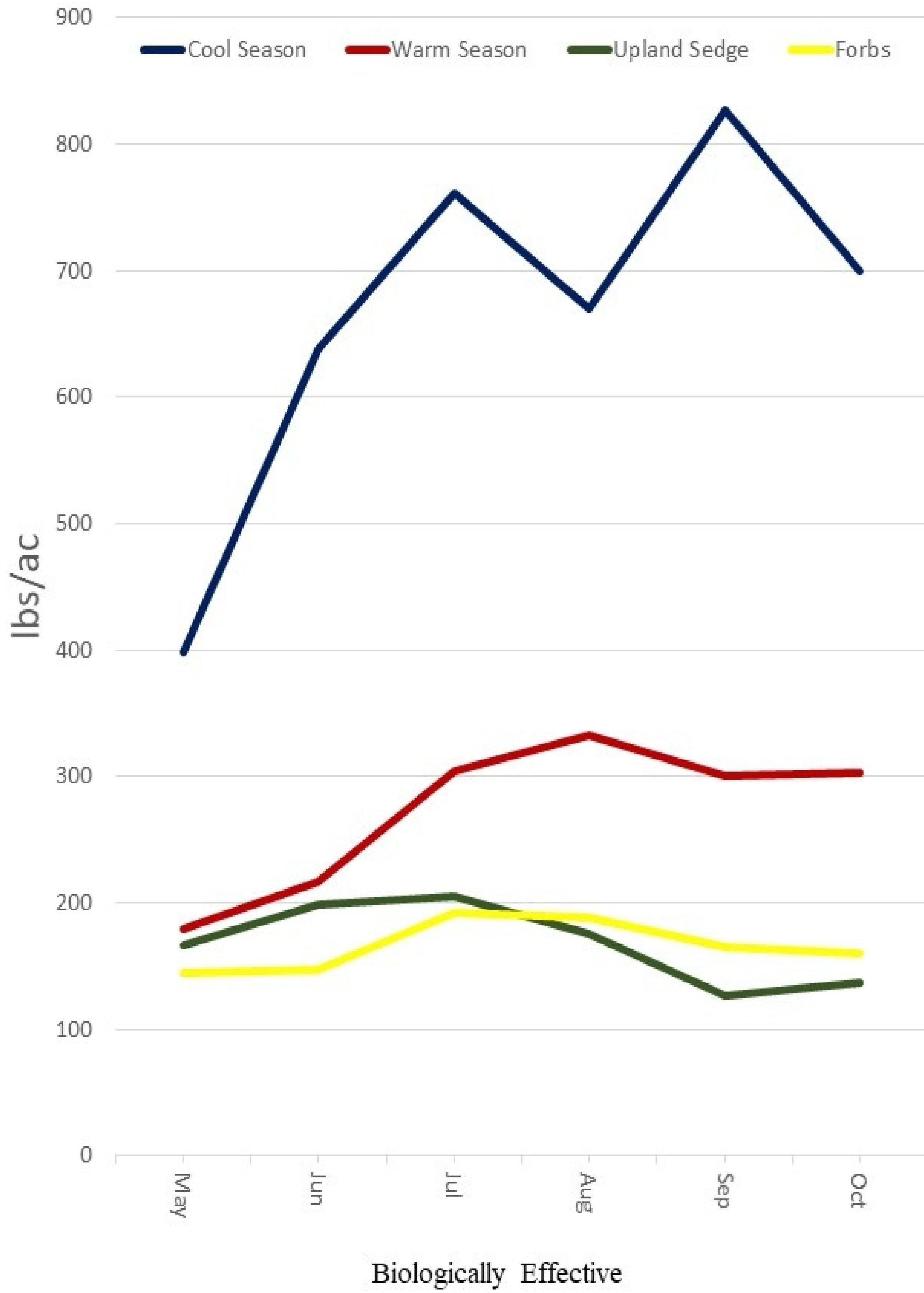

Figure 3. Mean monthly herbage biomass (lbs/ac) by biotypes on the silty site of the Biologically Effective concept, 1983-2012.

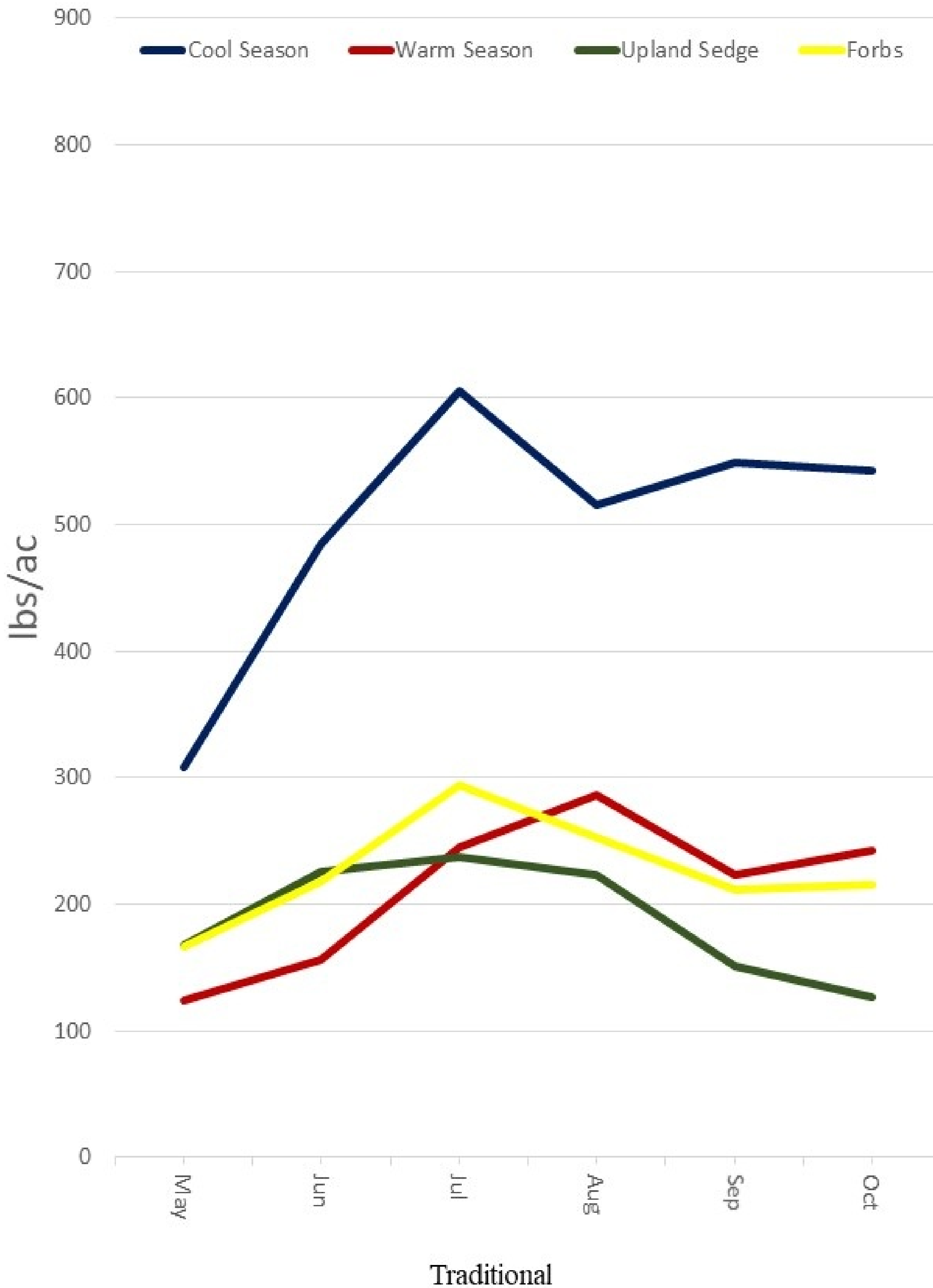

Figure 4. Mean monthly herbage biomass (lbs/ac) by biotypes on the silty site of the Traditional concept, 1983-2012.

Table 9. Mean monthly herbage biomass (lbs/ac) produced on the silty sites of the Biologically Effective concept compared to that of the Traditional concept, 1983-2012.

Concept System	May	Jun	Jul	Aug	Sep	Oct
Cool Season						
Biologically Effective	397.73	637.66	760.51	670.20	826.89	698.80
Traditional	308.46	483.96	606.10	515.39	548.70	542.12
% Difference	28.9	31.8	25.5	30.0	50.7	28.9
Warm Season						
Biologically Effective	179.90	217.06	304.30	333.21	300.86	302.53
Traditional	123.98	157.64	244.45	287.08	222.68	241.69
% Difference	45.1	37.7	24.5	16.1	35.1	25.2
Upland Sedge						
Biologically Effective	165.99	199.29	204.99	175.74	127.28	137.21
Traditional	168.26	226.16	237.83	222.50	151.45	126.55
% Difference	-1.3	-11.9	-13.8	-21.0	-16.0	8.4
Forbs						
Biologically Effective	145.26	146.55	193.27	187.79	164.72	159.88
Traditional	166.47	218.24	293.73	253.01	212.18	216.13
% Difference	-12.7	-32.9	-34.2	-25.8	-22.4	-26.0

Table 10. Mean grazing season (June to October) herbage biomass (lbs/ac) by biotype categories on the silty ecological site of the Biologically Effective and Traditional concepts, 1983-2012.

	Biologically Effective		Traditional		
Silty Site	Herbage Biomass lbs/ac	Composition %	Herbage Biomass lbs/ac	Composition %	Difference %
Cool Season	718.81	53.3	539.25	44.9	33.3
Warm Season	291.62	21.6	230.71	19.2	26.4
Upland Sedge	168.90	12.5	192.90	16.1	-12.4
Forbs	170.44	12.6	238.66	19.9	-28.6
Grasses	1010.43	74.9	769.96	64.1	31.2
Graminoids	1179.33	87.4	962.86	80.2	22.5
Total	1349.77		1201.52		12.3

Table 11. Basal cover (%) of graminoids on the silty sites of the Biologically Effective and Traditional concepts, 1983-2012.

	Biologically Effective		Traditional		
Silty Site	Basal Cover %	Composition %	Basal Cover %	Composition %	Difference %
Cool Season	7.02	24.6	5.85	28.5	20.0
Warm Season	15.95	55.9	8.76	42.6	82.1
Upland Sedge	5.55	19.5	5.95	28.9	-6.7
Grasses	22.97	80.5	14.61	71.1	57.2
Graminoids	28.52		20.56		38.7

Table 12. Percent reduction of herbage biomass production resulting from partial defoliation treatments prior to grass tiller 3.5 new leaf stage.

Date of Defoliation Treatment	Swift Current grazing data	Mandan clipping data	Dickinson grazing data
1 May	-78%	-76%	-
15 May	-46%	-57%	-45%

Swift Current data from Campbell 1952.
Mandan data from Rogler et al. 1962 and Lorenz (per.com.).
Dickinson data from 1982 to 1987 grazing studies.

Table 13. Primary tiller density resulting from control (0%), 50%, and 25% defoliation treatments on seasonlong and twice-over grazing management strategies at end of two growing seasons associated with available mineral nitrogen and rhizosphere volume.

	Tiller density at end of two growing seasons			Mineral Nitrogen	Rhizosphere Volume
Management Strategy	Control $\#/m^2$	June 50% $\#/m^2$	June 25% $\#/m^2$	kg/ha	cm^3/m^3
Seasonlong	313.3	156.6	250.7	85.9	1552.3
Twice-over	469.9	501.3	814.4	199.2	5212.9

Table 14. Density (#/m^2) of major tiller types resulting from control (0%) and 25% defoliation treatments on seasonlong and twice-over grazing management strategies during two growing seasons.

Two Growing Seasons Defoliation Treatment Management Strategy	First Year Carryover Tillers #/m^2	Initiated Vegetative Tillers #/m^2	Terminated Vegetative Tillers #/m^2	Terminated Flowering Tillers #/m^2	Total Different Tillers #/m^2	Second Year Remaining Tillers #/m^2
Control						
Seasonlong	188.0	657.8	250.6	125.3	845.8	469.9
Twice-over	626.5	1472.3	720.4	720.5	2098.8	657.9
June 25%						
Seasonlong	250.6	657.9	313.3	219.3	908.5	375.9
Twice-over	595.2	1660.4	877.2	344.6	2255.6	1033.8

Table 15. Density (#/m^2) of tiller types resulting from control (0%) and 25% defoliation treatments on seasonlong and twice-over grazing management strategies during the first and second growing seasons.

First Growing Season Defoliation Treatment Management Strategy			Live tillers early May #/m^2	New tillers first season #/m^2	Total first season tillers #/m^2	Tillers at flower stage #/m^2	Dead tillers first season #/m^2	Live tillers late season #/m^2	New fall tillers #/m^2	Live tillers mid October #/m^2	Dead tillers winter period #/m^2
Control											
Seasonlong			281.9	0.0	281.9	94.0	62.7	125.3	94.0	219.3	0.0
Twice-over			877.1	62.7	939.8	344.6	250.6	344.6	250.6	595.2	31.3
June 25%											
Seasonlong			438.6	31.3	469.9	94.0	156.6	219.3	125.3	344.6	0.0
Twice-over			971.1	62.7	1033.8	156.6	407.2	469.9	344.6	814.5	188.0
Second Growing Season Defoliation 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 stage #/m^2**	**Dead tillers second season #/m^2**	**Live tillers late season #/m^2**	**New fall tillers #/m^2**	**Live tillers mid October #/m^2**	
Control											
Seasonlong	219.3	188.0	407.2	125.3	532.5	31.3	188.0	313.3	156.6	469.9	
Twice-over	563.9	469.9	1033.8	250.6	1284.4	375.9	438.6	469.9	188.0	657.8	
June 25%											
Seasonlong	344.6	0.0	344.6	188.0	532.5	125.3	156.6	250.6	125.3	375.9	
Twice-over	626.5	469.9	1096.4	188.0	1284.4	188.0	281.9	814.5	219.3	1033.8	

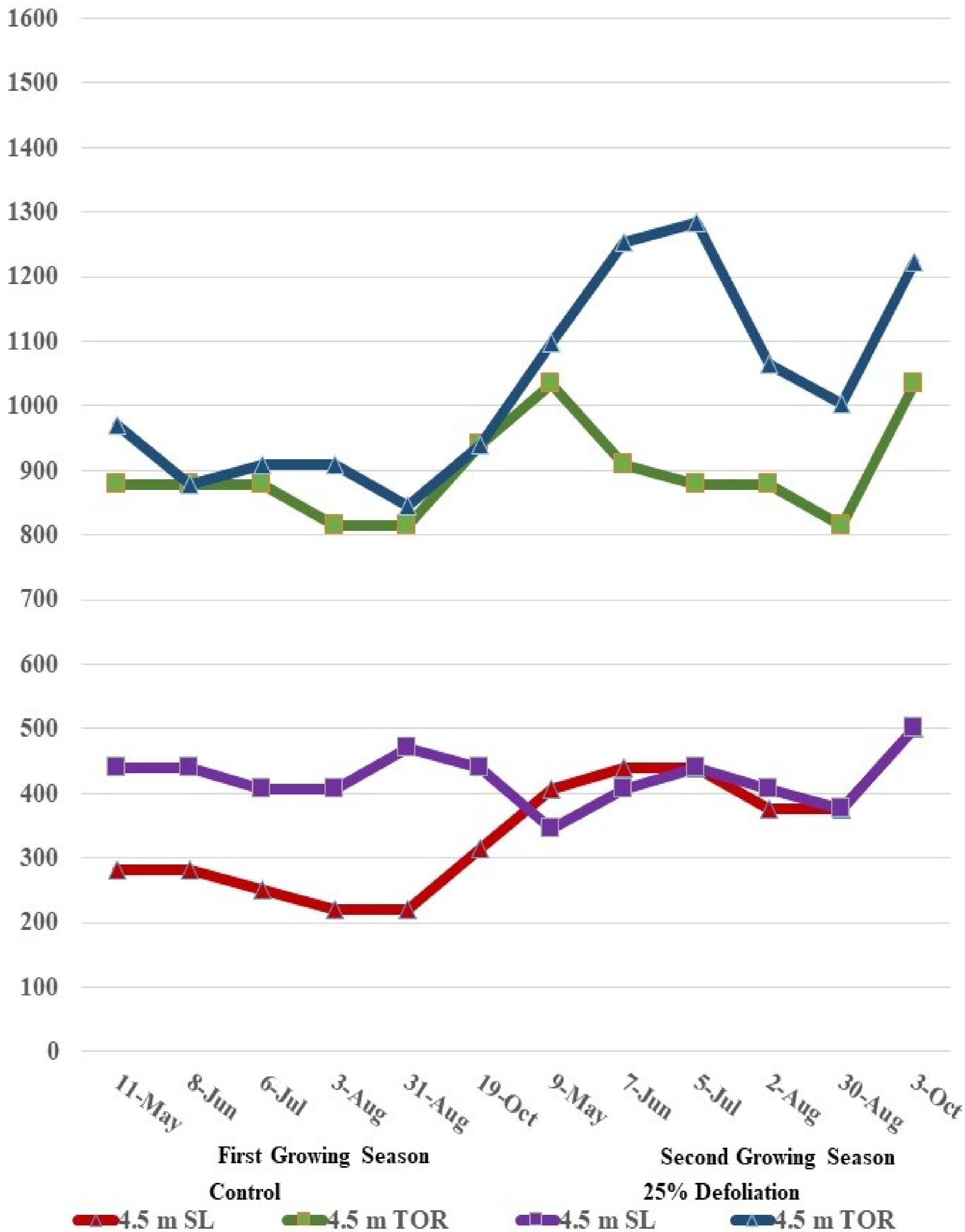

Figure 5. Monthly tiller density per square meter on the control and mid June 25% defoliation treatments during the first and second growing seasons.

Table 16. Density (#/m^2) of mean monthly tillers of pregrazing and grazing periods from control (0%) and 25% defoliation treatments on seasonlong and twice-over grazing management strategies during two growing seasons.

	First Growing Season		Second Growing Season	
Two Growing Seasons Defoliation Treatment Management Strategy	Pregrazing Tillers May #/m^2	Grazing Period Tillers Jun-mid Oct #/m^2	Pregrazing Tillers May #/m^2	Grazing Period Tillers Jun-mid Oct #/m^2
Control				
Seasonlong	281.9	245.4	407.2	391.6
Twice-over	877.1	814.5	1033.8	892.8
June 25%				
Seasonlong	438.6	402.0	344.6	391.6
Twice-over	971.1	824.9	1096.4	1117.3

Table 17. Density (#/m²) of initiated vegetative tillers from control (0%) and 25% defoliation treatments on seasonlong and twice-over grazing management strategies during two growing seasons.

Two Growing Seasons Defoliation Treatment Management Strategy	Spring Tillers mid Apr-May #/m²	Summer Tillers Jun-Jul #/m²	Fall Tillers Aug-mid Oct #/m²	Total Vegetative Tillers #/m²
Control				
Seasonlong	313.3	94.0	250.6	657.9
Twice-over	877.1	156.6	438.6	1472.3
June 25%				
Seasonlong	250.6	156.6	250.6	657.9
Twice-over	1033.8	62.7	563.9	1660.4

Table 18. Density (#/m²) of terminated vegetative tillers before reaching maturity and terminated lead tillers after flowering from control (0%) and 25% defoliation treatments on seasonlong and twice-over grazing management strategies during two growing seasons.

Two Growing Seasons Defoliation Treatment Management Strategy	Vegetative Tillers Spring mid Apr-May #/m²	Vegetative Tillers Grazing Period Jun-mid Oct #/m²	Lead Tiller Past Flowering Jun-mid Oct #/m²	Winter Dormancy Period #/m²	Total Terminated Tillers #/m²
Control					
Seasonlong	0.0	250.6	125.3	0.0	375.9
Twice-over	281.9	407.2	720.5	31.3	1440.9
June 25%					
Seasonlong	0.0	313.3	219.3	0.0	532.6
Twice-over	125.3	563.9	344.6	188.0	1221.8

Table 19. Density (#/m²) of mean monthly tiller types from control (0%) and 25% defoliation treatments on seasonlong and twice-over management strategies during two growing seasons.

Two Growing Seasons	Traditional Seasonlong		Twice-over Rotation	
Tiller Type	Control #/m²	mid June 25% #/m²	Control #/m²	mid June 25% #/m²
Reproductive	62.7	99.2	352.5	172.3
Vegetative	146.2	159.2	266.3	543.0
Secondary	133.1	156.6	279.3	334.2
Total Tillers	342.0	415.1	898.0	1049.4

Table 20. Density (#/m^2) of forage tillers between the 4 leaf stage and flower stage from control (0%) and 25% defoliation treatments on seasonlong and twice-over grazing management strategies means of two growing seasons.

	Biweekly Periods								
Two Growing Seasons Defoliation Treatment Management Strategy Tiller Type	E May #/m^2	M May #/m^2	E Jun #/m^2	M Jun #/m^2	E Jul #/m^2	M Jul #/m^2	E Aug #/m^2	L Aug #/m^2	M Oct #/m^2
Control									
Seasonlong									
Reproductive	15.6	31.3	47.0	15.6	15.6	0.0	0.0	0.0	0.0
Vegetative	15.6	47.0	78.3	109.6	156.6	156.6	156.6	156.6	156.6
Secondary	0.0	0.0	0.0	15.6	15.6	31.3	15.6	47.0	78.3
Total	31.3	78.3	125.3	141.0	188.0	188.0	172.3	203.6	235.0
Twice-over									
Reproductive	125.3	203.6	281.9	281.9	156.6	47.0	31.3	0.0	0.0
Vegetative	47.0	78.3	188.0	250.6	266.3	266.3	235.0	235.0	235.0
Secondary	31.3	141.0	78.3	62.7	109.6	141.0	172.3	125.3	156.6
Total	203.6	422.9	548.2	595.2	532.5	454.2	438.6	360.3	391.6
June 25%									
Seasonlong									
Reproductive	15.6	47.0	62.7	47.0	31.3	0.0	0.0	0.0	0.0
Vegetative	47.0	94.0	141.0	156.6	156.6	156.6	156.6	125.3	125.3
Secondary	0.0	0.0	0.0	0.0	31.3	31.3	31.3	109.6	94.0
Total	62.7	141.0	203.6	203.6	219.3	188.0	188.0	234.9	219.3
Twice-over									
Reproductive	78.3	141.0	172.3	141.0	62.7	15.6	0.0	0.0	0.0
Vegetative	188.0	375.9	532.5	579.5	516.9	516.9	516.9	485.6	485.6
Secondary	15.6	0.0	15.6	47.0	203.6	156.6	141.0	141.0	203.6
Total	281.9	516.9	720.5	767.5	783.2	689.2	657.8	626.6	689.2

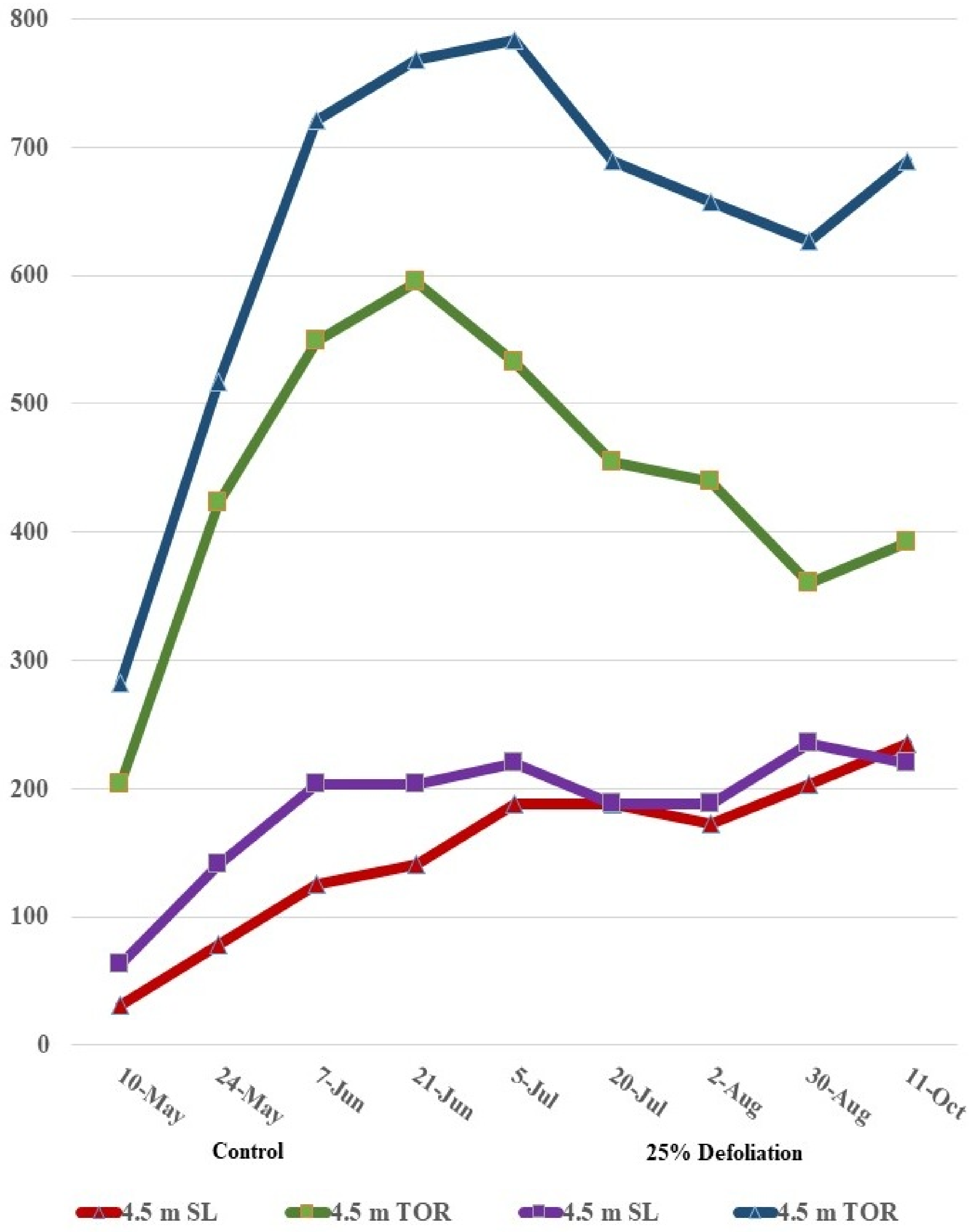

Figure 6. Density (#/m^2) of forage tillers between the 4 leaf stage and flower stage.

Table 21. Density (#/m^2) and percentage of forage tillers and not forage tillers from control (0%) and 25% defoliation treatments on seasonlong and twice-over management strategies.

Two Growing Seasons Defoliation Treatment Management Strategy	First Grazing Period early Jun to mid Jul Forage Tillers #/m^2	Not Forage Tillers #/m^2	Total Tillers #/m^2	Second Grazing Period mid Jul to mid Oct Forage Tillers #/m^2	Not Forage Tillers #/m^2	Total Tillers #/m^2	Total Grazing Period early Jun to mid Oct Forage Tillers #/m^2	Not Forage Tillers #/m^2	Total Tillers #/m^2
Control									
Seasonlong	160.6	191.9	352.5	199.7	134.5	334.2	179.0	162.5	341.5
% of total	45.6%	54.4%		59.8%	40.2%		52.4%	47.6%	
Twice-over	532.5	352.5	885.0	411.2	471.2	882.4	474.4	409.0	883.4
% of total	60.2%	39.8%		46.6%	53.4%		53.7%	46.3%	
June 25%									
Seasonlong	203.6	219.3	422.9	207.6	225.7	433.3	208.1	221.1	429.2
% of total	48.1%	51.9%		47.9%	52.1%		48.5%	51.5%	
Twice-over	740.1	340.7	1080.8	665.7	331.5	997.2	704.9	325.8	1030.7
% of total	68.5%	31.5%		66.8%	33.2%		68.4%	31.6%	

Table 22. Mean monthly native (cool and warm season) grass biomass (lbs/ac) on silty ecological sites of the seasonlong and twice-over management strategies, 1983-2012.

Silty Site	Jun	Jul	Aug	Sep	Oct	Mean
Twice-over	854.72	1064.94	1003.41	1127.75	1001.33	1010.43
Seasonlong	641.60	850.55	802.47	771.38	783.81	769.96
Difference	213.12	214.39	200.94	356.37	217.52	240.47
% increase from twice-over	33.2	25.2	25.0	46.2	27.8	31.2

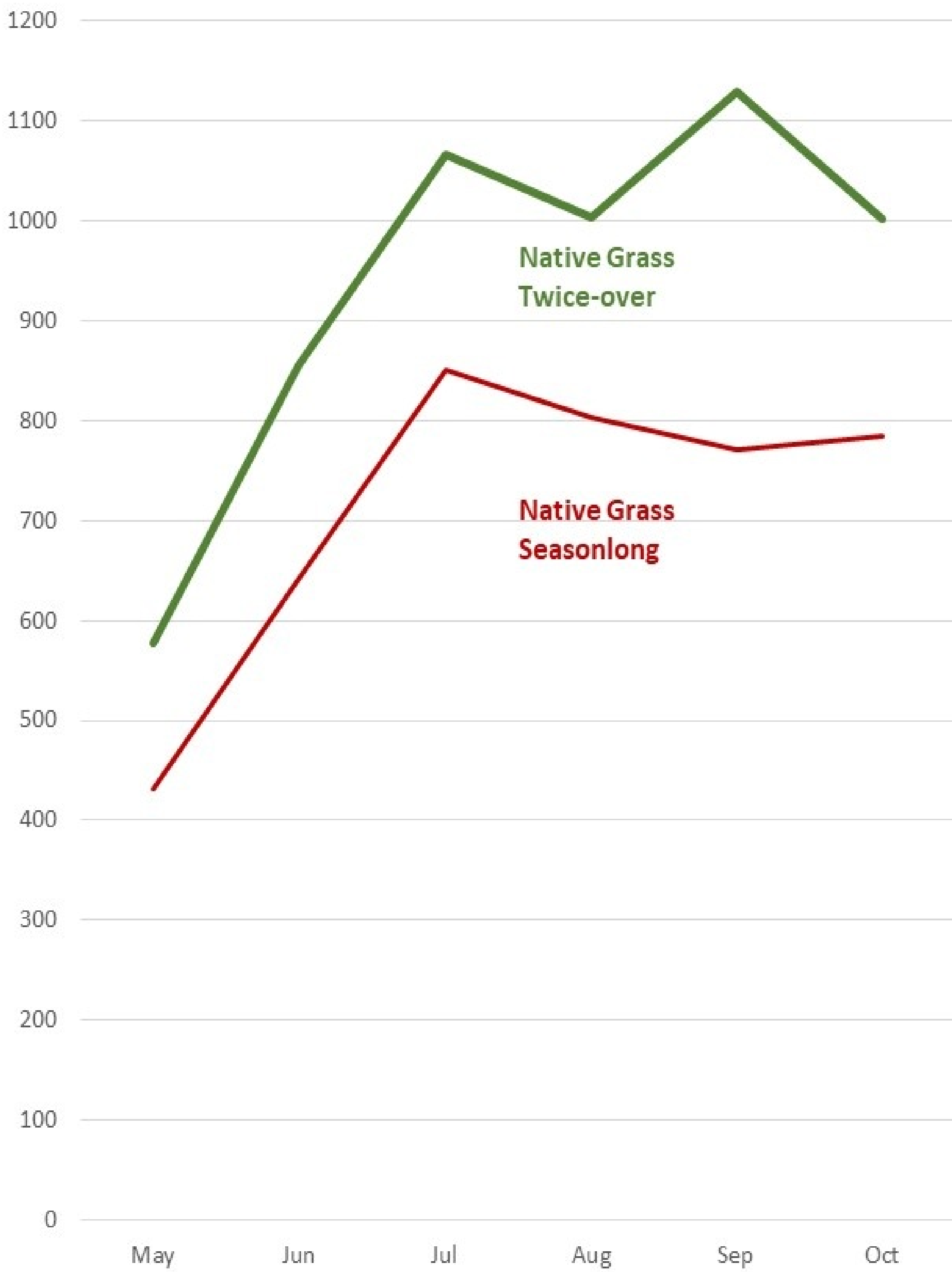

Figure 7. Mean monthly native grass biomass (lbs/ac) on seasonlong and twice-over management strategies.

Table 23. Percent crude protein on native rangeland summer pastures.

Grass Biotype	May		Jun		Jul		Aug		Sep		Oct
	8	24	8	24	8	24	8	24	8	24	15
Upland Sedge		13.8	13.6	11.7	10.4	8.9	7.8	7.6	8.0	6.8	6.9
Cool Season											
Lead Tillers		16.4	14.8	13.7	10.9	8.9	6.9	6.6	5.3	6.4	6.0
Secondary Tillers					10.2		11.6		13.2	12.1	6.1
Warm Season											
Lead Tillers		15.6	13.9	12.2	10.8	8.9	7.3	7.1	6.5	4.5	4.4
Secondary Tillers							8.9		10.0	8.2	5.7
Native Grass											
Lead Tillers		15.8	14.3	12.9	10.8	8.9	7.3	7.1	6.6	5.9	5.8
Secondary Tillers					10.2		10.3		11.6	10.2	5.9

Data summarized from Whitman et al. 1951 and Sedivec 1999.

Table 24. Percent phosphorus on native rangeland summer pastures.

Grass Biotype	May		Jun		Jul		Aug		Sep		Oct
	8	24	8	24	8	24	8	24	8	24	15
Upland Sedge		0.169	0.160	0.166	0.154	0.122	0.103	0.105	0.110	0.083	0.090
Cool Season											
Lead Tillers		0.238	0.256	0.238	0.217	0.188	0.153	0.147	0.122	0.120	0.118
Secondary Tillers					0.274	0.284	0.275	0.228	0.243	0.258	
Warm Season											
Lead Tillers		0.248	0.293	0.281	0.245	0.219	0.181	0.172	0.147	0.105	0.081
Secondary Tillers						0.285	0.270	0.270	0.254	0.251	
Native Grass											
Lead Tillers		0.232	0.261	0.252	0.222	0.194	0.158	0.153	0.125	0.108	0.096
Secondary Tillers					0.274	0.285	0.273	0.249	0.249	0.255	

Data summarized from Whitman et al. 1951.

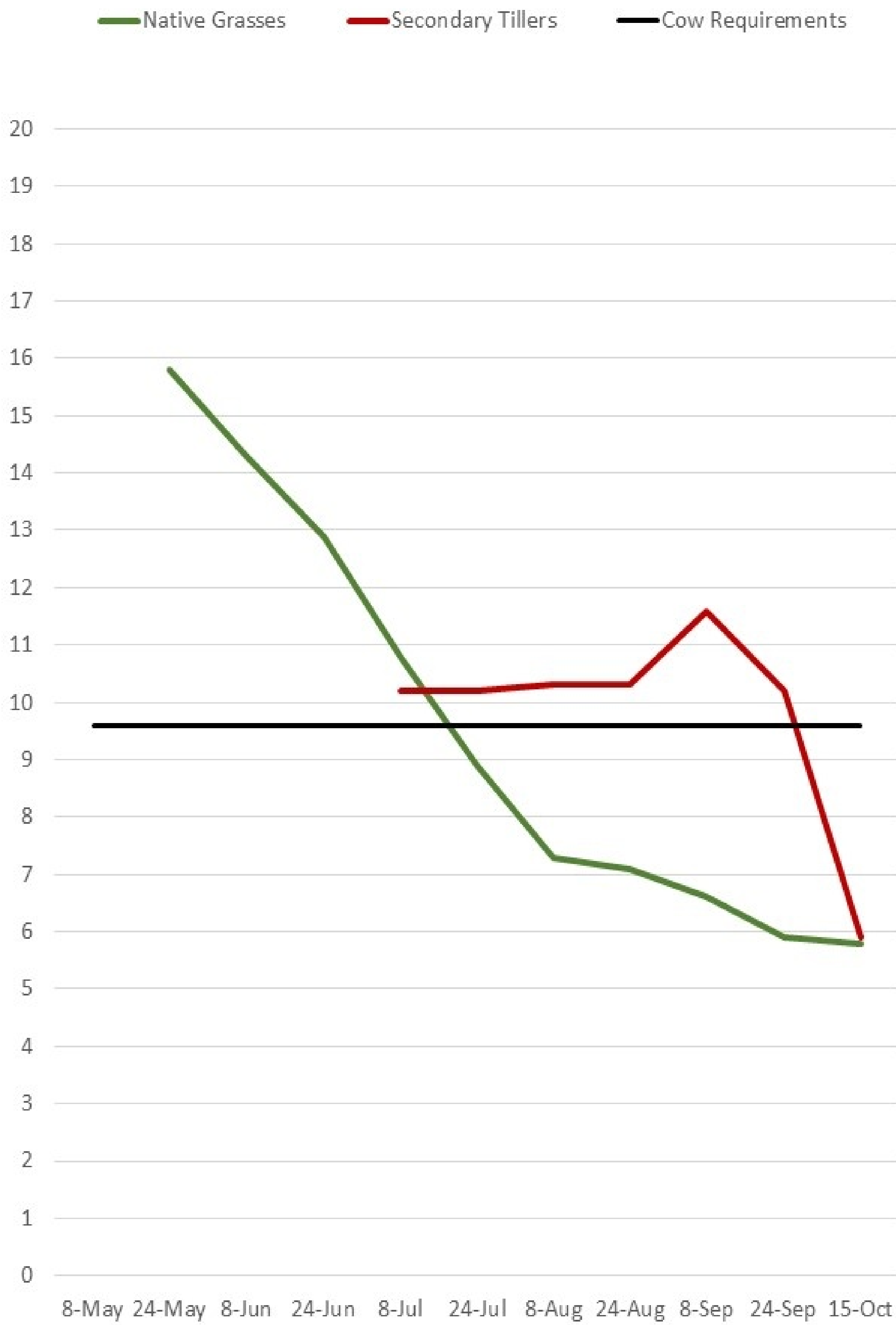

Figure 8. Percent Crude Protein of lead tillers and secondary tillers during the growing season. Data from Whitman et al. 1951 and Sedivec 1999.

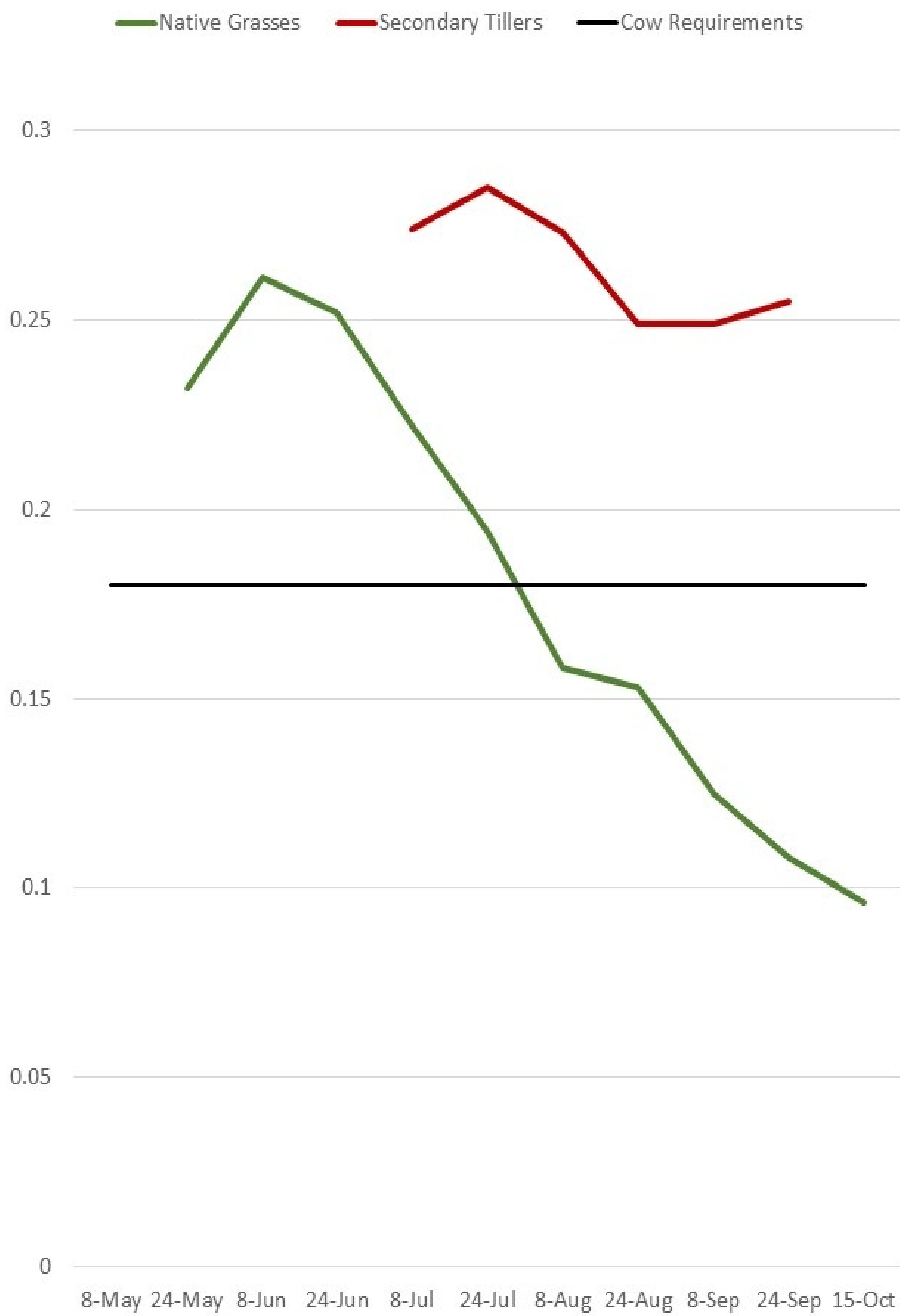

Figure 9. Percent Phosphorus of lead tillers and secondary tillers during the growing season. Data from Whitman et al. 1951.

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