BIOGEOCHEMICAL PROCESSES OF PRAIRIE ECOSYSTEMS

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Biogeochemical Processes of Prairie Ecosystems
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Biology of Defoliation by Grazing

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Management of grassland ecosystems has customarily been applied from the perspective of the "use" of the grassland, e.g. for wildlife habitat or for livestock forage. Placing management priority on the use of a grassland ecosystem imposes antagonistic effects on grassland plants and soil organisms that causes degradation of biogeochemical processes and reduction of grassland productivity. Management strategies that place priority with the living components of the ecosystem meet the biological requirements of grassland plants and soil organisms, and are beneficial for biogeochemical processes, thereby enhancing health and productivity of grassland ecosystems.

Implementation of biologically effective management strategies that are beneficial for grassland ecosystems requires knowledge of grass developmental morphology and physiological processes that help grass tillers withstand and recover from defoliation, and requires an understanding of the symbiotic relationship among rhizosphere organisms, grass plants, and large grazing herbivores. This report is a compilation of scientific knowledge about the biology of defoliation by grazing and the application of biologically effective defoliation to grassland ecosystems.

Grass Tiller Development

Grass tillers consist of shoots and roots. The shoot is the stem and leaves, and comprises repeated structural units called phytomers (Beard 1973, Dahl 1995). A phytomer consists of a leaf, with a blade and a sheath separated by a collar; a node, the location of leaf attachment to the stem; an internode, the stem between two nodes; and an axillary bud, meristematic tissue capable of developing into a new tiller (Hyder 1974, Dahl and Hyder 1977). Each tiller shoot generally produces 6 to 8 phytomers per growing season (Langer 1972, Dahl 1995). The crown of a grass tiller is the lower portion of a shoot and has two or more nodes (Dahl 1995). Fibrous roots grow from crown nodes that are located below ground. The internodes of the crown nodes associated with roots, crown tillers, and rhizome tillers do not elongate (Dahl 1995).

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). The oldest cells of a leaf are at the tip, and the youngest cells are at the base (Langer 1972, Dahl 1995). Several leaf primordia are at various stages of development at any one time. The oldest leaf is outermost, while younger leaves grow up through existing leaf sheaths (Rechenthin 1956, Beard 1973). Growth of the leaf results through cell enlargement and elongation (Esau 1960, Dahl 1995). A few new cells are produced by intercalary meristem located at the base of the blade, the base of the sheath, and the base of the internode (Esau 1960). Cell expansion occurs in the region protected by the sheaths of older leaves. When the cells emerge and are exposed to light, expansion ceases and photosynthesis and transpiration begin (Langer 1972). Once a leaf blade is fully expanded, no further growth of that blade is possible (Dahl 1995).

Individual leaves of grass tillers are relatively short lived. Young middle-aged leaves are in their prime when the rate of apparent photosynthesis is maximum and the leaves begin exporting assimilates to other parts (Langer 1972). At this point, the leaf has its greatest dry weight. Leaf senescence, or aging, begins shortly after middle age. Senescence begins at the tip, the oldest part of the leaf, and spreads downward. As senescence progresses, apparent photosynthesis and movement of assimilates from the leaf to the other parts of the plant decrease (Langer 1972). The rate of senescence occurs at about the same rate as leaf appearance but is influenced by environmental conditions. During senescence, cell constituents are mobilized and redistributed to other parts of the plant (Beard 1973). This process causes weight of the leaf to decrease (Leopold and Kriedemann 1975). The percentage of dryness in a leaf blade is an indication of the degree of senescence.

Longevity of grass tillers generally does not exceed two growing seasons (Langer 1956, Butler and Briske 1988). Production of new leaf primordia continues until the status of the apical meristem changes from vegetative to reproductive. Sexual reproductive growth can begin after the tiller has attained a certain minimum amount of vegetative development (Dahl 1995). Initiation of the reproductive growth stage is triggered by photoperiod (Roberts 1939, Leopold and Kriedemann 1975, Dahl 1995) but can be slightly modified by temperature and precipitation (McMillan 1957, Leopold and Kriedemann 1975, Dahl and Hyder 1977). Most tillers initiate vegetative growth during the previous growing season, overwinter, resume growth the subsequent growing season, become florally induced, and proceed with development of sexual reproductive structures (Briske and Richards 1995). When the florally induced grass tiller is between the third new leaf stage and 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). Previously formed leaf buds continue to grow and develop (Esau 1960, Langer 1972). Many domesticated cool-season grasses reach the three and a half new leaf stage around late April to early or mid May. Most native cool-season grasses reach the three and a half new leaf stage around early June, and most native warm-season grasses reach the three and a half new leaf stage around mid June (Manske 1999a).

Grass tillers exhibit short shoot and long shoot strategies of stem elongation. Grasses with short shoots do not produce significant internode elongation during vegetative growth and the apical meristem remains below grazing or cutting height. Production of new leaf primordia continues until the apical meristem changes to reproductive status and developing leaves continue to expand until the flower stalk elongates (Dahl 1995). Grasses with long shoots elevate the apical meristem a short distance above ground level by internode elongation while still in the vegetative phase (Dahl 1995). After the apical meristem has changed from vegetative status, additional stem elongation occurs during the sexual reproductive phase. Vegetative tiller production from axillary buds is stimulated in grasses with long shoots by defoliation that removes the elevated apical meristem prior to flowering (Richards et al. 1988). However, production from the developing leaf primordia on the removed apical meristem is lost to the ecosystem. Grass species with long shoot tillers are nearly always decreased in pastures that are repeatedly grazed heavily (Branson 1953).

The flower bud primordia develop into the inflorescence, with the apical dome becoming the terminal spikelet. The first external evidence of flower stalk development is swelling of the enclosing sheath known as the "boot" stage. During the head emergence phenophase, 4 or 5 of the upper internodes, along with the attached leaf sheaths, elongate very rapidly by intercalary meristem cell development and the inflorescence reaches near-maximum height. The flowering (anthesis) phenophase occurs when the feathery stigmas (female parts) spread out and the anthers (male parts) are exposed (Langer 1972). Cool-season grasses with the C_3 photosynthetic pathway are long-day plants and reach the flowering phenophase before 21 June during the period of increasing day length. Warm-season grasses with the C_4 photosynthetic pathway are short-day plants and reach the flowering phenophase after 21 June during the period of decreasing day length and increasing night length (Weier et al. 1974, Leopold and Kriedemann 1975). The life cycle of a tiller with the apical meristem status changed to reproductive terminates during that growing season (Briske and Richards 1995).

Procurement of Elemental Resources

Growth in grass plants requires procurement of essential elements from the surrounding environment. Phosphorus and minor mineral nutrients are absorbed by grass plant roots from soil with assistance from endomycorrhizal fungi. The major elements needed by plants are hydrogen, carbon, and nitrogen.

The hydrogen comes from soil water (H_2O) absorbed through the roots and distributed throughout the plant within the xylem vascular tissue. When the rate of water absorption by the roots is less than the rate of water loss from transpiration through stomata openings, plant tissue develops water stress. Plant water stress limits growth. Plant water stress can be reduced with implementation of biologically effective management practices by increasing the soil water holding capacity and by reducing soil water loss through evapotranspiration. Increased biomass and activity of both endomycorrhizal and ectomycorrhizal fungi improve soil aggregation that increases soil pore spaces, increases water infiltration, increases water holding capacity, increases soil depth, and improves drought tolerance. Increased grass plant density and increased litter cover lowers soil temperature reducing soil water loss through evaporation.

The source of carbon for plant growth is atmospheric carbon dioxide (CO_2). Plants capture and fix carbon with the hydrogen from soil water during the process of photosynthesis which converts energy from the sun into chemical energy. Capturing energy by fixing carbon has a relatively low impact on organisms that possess chlorophyll and has low biological costs to the ecosystem resources. The assimilated carbon is combined in several ways to form various types of sugars and starches that collectively are carbohydrates (CH_2O). Some of the carbohydrates are used in growth as structural components, some are used in formation of compounds of greater complexity, and some are used for energy resulting from respiration; the remaining carbohydrates are nonstructural carbohydrates that can be stored for later use when these processes are operational during the winter hardening process. Plant carbohydrates can be used as an energy source by herbivores that consume grass plant parts. Carbohydrates and carbon compounds are broken down to carbon dioxide (CO_2) by respiration or by death and decay of plant parts or of herbivore body parts and by decay of herbivore excreta.

The source of nitrogen for plant growth is mineral nitrogen ($NO_{3,}$ NH_4) converted from soil organic nitrogen by rhizosphere organisms. Low quantities of available mineral nitrogen limits productivity more often than water on grassland ecosystems (Tilman 1990). Increasing rhizosphere organism activity increases the quantity of available mineral nitrogen. Mineral nitrogen is absorbed by plant roots. The grass plant uses mineral nitrogen to produce proteins. Plant crude protein can be used by herbivores that consume grass plant parts. Organic nitrogenous compounds comprising herbivore excreta or dead plant material are returned to grassland soils. Transforming nitrogen from organic nitrogen to mineral nitrogen and back to organic nitrogen is complex and has a great impact on many organisms at multiple trophic levels and has high biological costs on the ecosystem resources.

Defoliation Resistance Mechanisms

The key factor in meeting grass plant biological requirements is proper timing of 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 processes in all parts of the plant; alters the plant community microclimate by changing light transmission, moisture relations, and temperature; and changes the soil environment, thereby affecting soil organism activity (Manske 2000a). Grass plants have developed defoliation resistance mechanisms in response to grazing during the period of coevolution with herbivores (McNaughton 1979, 1983; Coleman et al. 1983; Briske 1991; Briske and Richards 1995; Manske 1999a). The defoliation resistance mechanisms help grass tillers withstand and recover from partial defoliation by grazing. These mechanisms are: herbivore-induced compensatory physiological processes (McNaughton 1979, 1983; Briske 1991); stimulation of vegetative reproduction of secondary tillers from axillary buds (Mueller and Richards 1986, Richards et al. 1988, Murphy and Briske 1992, Briske and Richards 1994, Briske and Richards 1995); and stimulation of rhizosphere organism activity and the increased conversion of mineral nitrogen from soil organic nitrogen (Coleman et al. 1983, Ingham et al. 1985).

Compensatory Physiological Processes

Compensatory physiological processes are triggered by seasonable partial defoliation by grazing of grass tillers during phenological growth between the three and a half new leaf stage and the flowering (anthesis) stage. Compensatory physiological processes activate: increased growth rates of replacement leaves and shoots that produces larger leaves with greater mass (Langer 1972, Briske and Richards 1995); increased photosynthetic capacity of remaining mature leaves and rejuvenated portions of older leaves not completely senescent (Atkinson 1986, Briske and Richards 1995); and increased allocation of carbon and nitrogen from remaining leaf and shoot tissue, not from material stored in the roots (Richards and Caldwell 1985, Briske and Richards 1995, Coyne et al. 1995).

Activity of meristematic tissue is enhanced and growth rates of replacement leaves and shoots increases following partial defoliation. The rate of leaf area expansion following defoliation is determined by interactions among meristem type, environmental variables, and resource availability (Briske and Richards 1995). Growth is most rapid from intercalary meristem, intermediate from apical meristem, and slowest from axillary buds (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). The photosynthetic rate of the replacement leaves is higher than that of same-age foliage on undefoliated tillers (Briske and Richards 1995).

Defoliated tillers increase photosynthetic rates of remaining foliage (Briske and Richards 1995). This compensatory photosynthesis can be induced by changes in light quality and intensity that result from grazing modifications in the microhabitat and by modifications of physiological functions caused by the indirect effects resulting from increased root-shoot ratio and mediated by cytokinins and other signals produced in the root (Briske and Richards 1995). These changes appear to affect leaf development and aging. The photosynthetic apparatus is rejuvenated, the leaf senescence rate is inhibited or reduced, and the lifespan of leaves is increased (Briske and Richards 1995). Remaining mature leaves on defoliated tillers frequently develop increased leaf mass per unit area shortly after defoliation (Briske and Richards 1995).

Compensatory physiological processes related to increased growth of replacement leaves and increased photosynthetic and physiological activity in remaining leaves requires an abundant supply of carbon and nitrogen. The normal processes through which the plant acquired these elements is affected by the defoliation event and alternative sources are required (Coyne et al. 1995). Most of the carbon allocation for compensatory growth processes comes not from stored material in the roots but comes from the remaining shoot tissue and current fixed carbon from photosynthesis (Richards and Calwell 1985, Briske and Richards 1995). Very little, if any, of the root carbon is remobilized to support shoot growth (Briske and Richards 1995). Current photosynthetic carbon from the remaining shoot is preferentially allocated to areas of active shoot meristematic tissue and is more important for plant growth following defoliation than are carbohydrate reserves (Ryle and Powell 1975, Richards and Caldwell 1985, Briske and Richards 1995, Coyne et al. 1995). Carbon allocation from undefoliated tillers to defoliated tillers increases following defoliation until the defoliated tillers reestablish their own photosynthetic capacity (Briske and Richards 1995).

Nitrogen pools in the remaining shoot tissue and roots can be mobilized to support shoot growth following defoliation (Briske and Richards 1995). Most of the remobilized nitrogen is allocated from remaining shoot tissue; only a small portion is allocated from material stored in the root system (Briske and Richards 1995). The amount of remobilized nitrogen from the remaining shoot is greatly reduced when greater quantities of mineral nitrogen are available in the media around the roots (Millard et al. 1990, Ourry et al. 1990). The increased available mineral nitrogen converted from soil organic nitrogen by active rhizosphere organisms is preferentially absorbed and moved to areas of active shoot meristmatic tissue soon after partial defoliation. A threshold quantity of 100 pounds per acre or greater of mineral nitrogen processed by the rhizosphere organisms is required for full activation of the compensatory physiological processes in partially defoliated grass tillers (Manske 2009, 2010).

Compensatory physiological processes are not fulfilled instantaneously and require some time to develop and perform all specific steps successfully. Successive defoliation events that occur before sufficient time has elapsed, disrupt the processes and diminish the beneficial effects for the grass tiller and grassland ecosystem.

Vegetative Reproduction by Tillering

Vegetative secondary tillers develop from lead tillers by the process of tillering. A vegetative tiller is a shoot derived from growth of an axillary bud (Dahl 1995) and is a complete unit with roots, stem, and leaves. All young tillers are dependent on the lead tiller for carbohydrates until they have developed their own root systems and mature leaves (Dahl 1995). After secondary tillers become independent, they remain in vascular connection with other tillers of the grass plant (Moser 1977, Dahl and Hyder 1977, Dahl 1995). There are two types of tillering: crown tillers and rhizome or stolon tillers. Crown tillers grow vertically close to the lead tiller and within the enveloping leaf sheath, and tend to have a tufted or bunch-type growth habit (Dahl and Hyder 1977, Dahl 1995). Rhizome tillers penetrate the enveloping leaf sheath and grow horizontally below the soil surface away from the lead tiller for a distance before beginning vertical growth. Rhizome growth may be either continuous, producing tillers at progressive intervals, or terminal, producing one tiller when the apex turns up and emerges from the soil (Dahl 1995). The rhizome type of tillering results in the spreading or creeping growth habit of sod-forming plants (Dahl and Hyder 1977, Dahl 1995). If the horizontal growth is aboveground, it is a stolon (Dahl 1995). Stolons have continuous growth and form tillers at progressive nodes (Dahl 1995). Grass plants can produce both crown tillers and rhizome tillers. Generally, one tiller growth type is produced by a grass species more than the other tiller type. However, the expressivity of tiller type can be influenced by several growth factors and environmental conditions, and can be manipulated by defoliation management.

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 of lead tillers (Briske and Richards 1995). The physiological process by which the lead tiller exerts hormonal control over axillary bud growth is lead tiller (apical) dominance (Briske and Richards 1995). Tiller growth from axillary buds is inhibited indirectly by auxin, as the inhibiting hormone does not enter the axillary buds (Briske and Richards 1995). Auxin interferes with the metabolic function of cytokinin, a growth hormone (Briske and Richards 1995). Partial defoliation of young leaf material from grass tillers at phenological growth between the three and a half new leaf stage and the flower (anthesis) stage can stimulate vegetative growth of secondary tillers from axillary buds. Defoliation temporarily reduces the production of the blockage hormone, auxin (Briske and Richards 1994). This abrupt reduction of plant auxin in the lead tiller allows for cytokinin synthesis or utilization in multiple axillary buds, stimulating the development of vegetative tillers (Murphy and Briske 1992, Briske and Richards 1994). Several axillary buds develop into secondary tillers following partial defoliation of lead tillers at vegetative stages of phenological growth. Apparently, none of the developing secondary tillers have growth far enough advanced to take complete hormonal control over the other developing axillary buds.

Growth of several secondary tillers from axillary buds requires an abundant supply of carbon and nitrogen. The source of the carbon is not from stored carbohydrates, but from increased photosynthetic capacity of remaining mature leaves and rejuvenated portions of older leaves not completely senescent. The quantity of leaf area required to provide adequate quantities of carbon is 66% to 75% of the predefoliation leaf area. The source of nitrogen for growth of secondary tillers from axillary buds is not from stored nitrogen but is the mineral nitrogen in the rhizosphere that the microorganisms had converted from soil organic nitrogen. A threshold quantity of 100 pounds per acre of mineral nitrogen needs to be available to the partially defoliated grass tillers in order for full activation of the vegetative reproductive processes (Manske 2009, 2010).

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 from the potential of 5 to 8 buds. This developing secondary tiller produces auxin in the apical meristem and young developing leaves that hormonally suppresses development of additional axillary buds.

The longer axillary buds remain hormonally inhibited, the less likely they are to form tillers (Mueller and Richards 1986). The age of the meristematic tissue of the axillary buds that produce secondary tillers is the same age as the meristematic tissue that produce the lead tillers and, most likely, both the lead tiller and secondary tiller meristematic tissue was produced during the previous growing season. Axillary buds survive as long as the lead tiller remains alive. The lead tiller terminates life by senescence during the same growing season that the apical meristem changes from vegetative to reproductive status, and all unstimulated axillary buds terminate with the lead tiller.

Fall tillers are produced by cool-season grasses during the winter hardening process that starts around mid August. Warm-season grasses produce fall tiller buds that remain at or below ground level until the next growing season. The age of the meristematic tissue that produces fall tillers and fall tiller buds is one generation younger than the meristem that produced the lead tillers and secondary tillers. Secondary tillers with apical meristem remaining in the vegetative status, fall tillers, and fall tiller buds become lead tillers during the subsequent growing season.

Longevity of grass plants in grassland ecosystems is dependent on production of tillers through vegetative reproduction from axillary buds. Grass plant longevity of major northern species managed with traditional grazing practices is known to endure at least for 27 to 43 years (Briske and Richards 1995). Grass plant longevity would be expected to be greatly extended when biologically effective grazing management specifically designed to stimulate the vegetative reproduction mechanisms is implemented.

Rhizosphere Organism Activity

The biogeochemical processes of the nitrogen cycle in grassland ecosystems that convert nitrogen into the various forms are a function of the interactions among rhizosphere organisms, grass plants, and large grazing herbivores. Soil organic matter of mixed grass prairie ecosystems generally contains about three to eight tons of organic nitrogen per acre. Organic nitrogen is a form of nitrogen not directly usable by grass plants. Organic nitrogen must be converted into inorganic (mineral) nitrogen in order to be usable by plants. In grassland ecosystems, the conversion of plant usable mineral nitrogen from soil organic nitrogen requires active rhizosphere organisms. Rhizosphere organism activity requires short chain carbon exudates from roots of grass plants. Rhizosphere organisms trade nitrogen to grass plants for carbon, and grass plants trade carbon to soil microorganisms for nitrogen. This interdependent symbiotic relationship between grass plants and rhizosphere organisms is controlled by partial defoliation of aboveground plant parts by large grazing herbivores.

The rhizosphere is the narrow zone of soil around active roots of perennial grassland plants and is comprised of bacteria, protozoa, nematodes, springtails, mites, endomycorrhizal fungi (Elliot 1978, Anderson et al. 1981, Harley and Smith 1983, Curl and Truelove 1986, Whipps 1990, Campbell and Greaves 1990) and ectomycorrhizal fungi (Caesar-TonThat et al. 2001b, Manske and Caesar-TonThat 2003). Rhizosphere organism biomass and activity are limited by access to simple carbon chains (Curl and Truelove 1986) because the microflora trophic levels lack chlorophyll and have low carbon (energy) content. Partial defoliation of grass plants at vegetative phenological growth stages by large grazing herbivores causes greater quantities of exudates containing simple carbon compounds to be released through the plant roots into the rhizosphere (Hamilton and Frank 2001). With the increase in availability of carbon compounds in the rhizosphere, activity of the microorganisms increases (Elliot 1978, Anderson et al. 1981, Curl and Truelove 1986, Whipps 1990). The increase in rhizosphere organism activity causes an increase in microorganism biomass and an increase in rhizosphere volume (Gorder, Manske, and Stroh 2004).

The activity of rhizosphere organisms increases along the trophic hierarchy, starting with the bacteria. Bacteria are microscopic single-celled saprophitic organisms that consume large quantities of soil organic matter and are one of the primary producers of the rhizosphere. The increased biomass and activity of the bacteria elevates the concentration of carbon dioxide (CO_2) resulting in stimulation of activity in the other rhizosphere organisms. Protozoa are single-celled microorganisms that are mainly small amoeba and feed primarily on bacteria. Nematodes are a diverse group of small nonsegmented worms. Most nematodes feed primarily on bacteria or fungi, some feed on protozoa, and some eat other nematodes. Springtails are the most abundant insect in grassland soils and they travel among rhizosphere structures. Minute springtails ingest considerable quantities of soil organic matter in order to eat fungi and bacteria. Mites are small eight-legged arachnids that travel among rhizosphere structures and feed on fungi, nematodes, small insects, and other mites. Mites help distribute fungus spores and bacteria through the soil by carrying them on their exoskeleton. Endomycorrhizal fungi are the other primary producers of the rhizosphere and are achlorophyllous saprophytes that live on dead organic matter and can not fix carbon because they lack chlorophyll. The bacteria and fungi are the microflora saprotrophic organisms at the bottom of the food chain and makeup the greatest biomass of the rhizosphere. Both bacteria and fungi contain high proportions of nitrogen in relation to their carbon content. The rhizosphere organisms of the microfauna trophic levels graze on bacteria or fungi and ingest greater quantities of nitrogen than they need for a balanced diet based on energy (carbon); the excess nitrogen is excreted as ammonium (NH_4). The primary symbiotic function of the endomycorrhizal fungi is to nitrify the ammonium (NH_4) excreted by rhizosphere organisms and convert it into nitrate (NO_3), which is a form of mineral nitrogen usable by grass plants. The elevated rhizosphere organism activity caused by the increase in available carbon compounds results in a greater quantity of organic nitrogen converted into mineral nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005).

Mineral nitrogen is absorbed by plant roots from the surrounding rhizosphere and, through complex processes, the plant combines the mineral nitrogen with carbon, hydrogen, and oxygen to synthesize different kinds of amino acids which are combined into large organic compounds to produce various types of proteins. The increase in mineral nitrogen available to a defoliated grass plant allows the plant to recover more quickly from defoliation, to accelerate the growth rate, and to increase the total herbage biomass production (Manske 1999a, 2003c). Organic nitrogen is returned back to grassland ecosystems contained within the organic matter from herbivore excreta and dead plant material that falls to the soil.

Along with the improvement of ecosystem biogeochemical processes and the resulting increase in available mineral nitrogen, the increase of mycorrhizal fungi biomass and activity benefits other grassland ecosystem functions. Endomycorrhizal fungi develop arbuscules, vesicles, and hyphae within root tissue of the host plant (Harley and Smith 1983) and secrete adhesive polysaccharides that bond soil particles around grass roots forming the structural environment for rhizosphere organisms, and the adhesive polysaccharides bind soil into aggregates resulting in increased soil pore spaces, increased water holding capacity, and increased rooting depth. Endomycorrhizal fungi also move phosphorus, other mineral nutrients, and water to the plant roots for absorption (Moorman and Reeves 1979, Harley and Smith 1983, Allen and Allen 1990, Box and Hammond 1990, Marschner 1992, Koide 1993, Marschner and Dell 1994, Smith and Read 1997). Ectomycorrhizal fungi develop a sheath around the root with hyphae and do not enter the tissue of the host plant (Harley and Smith 1983) and secrete large amounts of adhesive polysaccharides forming water-stable aggregates in soil that are water permeable but not water soluable, and the increased soil aggregation improves soil quality, increases soil oxygenation, increases water infiltration, and decreases erodibility (Caesar-TonThat and Cochran 2000, Caesar-TonThat et al. 2001a, Caesar-TonThat et al. 2001b, Caesar-TonThat 2002, Manske and Caesar-TonThat 2003).

Effects from Seasonality of Defoliation by Grazing

The effects of defoliation by grazing can be beneficial or antagonistic depending on the degree of foliage removal and phenological growth stage of the grass tiller. Seasonable defoliation places priority with the living components of the ecosystem and occurs at the proper time, between early June and mid October, to be beneficial and meet the biological requirements of the grass plants and soil organisms. Biologically effective defoliation that occurs during phenological growth between the three and a half new leaf stage and the flower (anthesis) stage triggers compensatory physiological processes in remaining leaf and shoot tissue, stimulates vegetative reproduction from axillary buds, and stimulates rhizosphere organism activity that increases available mineral nitrogen.

No Defoliation by Grazing

Full growing season rest and multiple season resting are antagonistic management choices that withhold defoliation from grasslands. The term "rest" is a misnomer because the common inference that "resting" a grassland by removal of defoliation causes revitalization of crucial processes is inaccurate. Resting a grassland by withholding defoliation causes regression of ecosystem biogeochemical processes and results in the deterioration of grassland ecosystems. Two negative changes occur relatively soon after grazing management is removed; live root biomass decrease (Whitman 1974, Brand and Goetz 1986) and standing dead leaves accumulate (Brand and Goetz 1986). The reduction of active root surface area causes a reduction in root length for interaction with rhizosphere organisms and causes a decrease in absorption of water and nutrients from the soil, resulting in a reduction in growth of aboveground plant parts. The accumulating standing dead leaves shade the lower leaves, increasing the rate of leaf senescence and reducing the rate of photosynthesis, causing a decrease in the supply of carbohydrates that results in a reduction in growth of leaves and roots (Langer 1972, Briske and Richards 1995). Grass leaves grown under shaded conditions become longer but narrower, thinner (Langer 1972, Weier et al. 1974) and lower in weight (Langer 1972) than leaves in sunlight. Shaded grass plants shift to erect growth forms with a small number of larger tillers (Briske and Richards 1995). Lack of grazing reduces grass tiller densities by decreasing tiller development and increasing tiller mortality through shading (Grant et al. 1983). After a few years, shading reduces the composition of native grass species in the ecosystem and increases the composition of shade-tolerant or shade-adapted replacement species, like smooth bromegrass and Kentucky bluegrass.

Standing dead material not in contact with soil does not decompose through microbial activity. Dead plant material on nongrazed treatments breaks down slowly over several years by leaching and weathering, and builds up into a thick mulch layer. Thick mulch modifies soil temperatures, inhibits water infiltration, and ties up carbon and nitrogen that causes decreased mycorrhizal fungi and rhizosphere organism activity in the soil, slowing nutrient cycles and reducing the quantities of nutrients available for new plant growth (Manske 2000a). Removal of grazing from grasslands for one season or for several seasons is not beneficial and causes accumulations of standing dead leaf material and reductions of live root biomass, live aboveground herbage biomass, and live plant density as a result of antagonistic effects on rhizosphere organism activity and biogeochemical processes of the nitrogen cycle. Ostensibly, the rate of decline from antagonistic effects on nongrazed treatments is slower than that on the deferred grazing, 6.0-m seasonlong, and 4.5-m seasonlong treatments (Manske 2011b). However, the degree of deterioration to grassland ecosystems caused by the antagonistic effects from long-term nongrazed treatments of 40 years and more is greater than that from traditional grazing treatments (Manske 2003a).

Prae Seasonable Defoliation by Grazing

Preseasonable defoliation, before the three and a half new leaf stage (April and May), is antagonistic to grass tiller growth and development and to rhizosphere organism activity. Secondary tillers of cool-season and warm-season grasses with apical meristem status remaining vegetative and fall initiated cool-season grass tillers survive overwinter on carbohydrate reserves that were stored by the tiller during the winter hardening process that occurs between mid August and mid October. Spring growth during the second growing season for these carryover tillers, reclassified as lead 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. Spring growth for fall developed tiller buds of warm-season grasses depends initially on carbohydrate reserves and later both on carbohydrate reserves and on photosynthetic product from new young leaves. Grass tiller growth and development depend, in part, on adequate carbohydrate reserves in early spring because the amount of photosynthetic product synthesized by the carryover leaves and the first couple of early growing new leaves is insufficient to meet the requirements for leaf growth (Heady 1975, 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 reduction of reserves during the winter respiration period, and the carbohydrate reserves remaining in the roots and crown are needed for both root growth and initial leaf growth during early spring. The low quantity of reserve carbohydrates may not be 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 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. Delays in spring grass growth are management-induced problems.

Defoliation of grass tillers during early spring activates no beneficial effects to the grassland ecosystem, exerts negligible stimulatory effects on vegetative tillering (Olson and Richards 1988, Vogel and Bjugstad 1968), and exudes little or no short chain carbon into the rhizosphere to stimulate microorganism activity. The remaining photosynthetically active leaf area following preseasonable defoliation is inadequate to replenish nonstructural carbohydrates and to support active leaf growth (Coyne et al. 1995). The quantity of herbage produced by a grass tiller after it has been prematurely grazed is dependent on the levels of carbohydrates present in the remaining plant at the time of defoliation (Coyne et al. 1995). Defoliation of the tiller before the three and a half new leaf stage results in greatly reduced growth rates of herbage production (Coyne et al. 1995) causing decreased peak herbage biomass later in the growing season (Manske 1994, 2000b). Grazing that starts in early May on native rangeland results in a reduction of more than 75% from the potential herbage biomass (Campbell 1952, Rogler et al. 1962, Manske 2000b). When grazing is started in mid May, 45% to 60% of the potential herbage biomass will not be produced that growing season (Campbell 1952, Rogler et al. 1962, Manske 2000b).

Early Seasonable Defoliation by Grazing

Removal of some foliage is needed to trigger the compensatory processes that help grass tillers withstand and recover from defoliation. Early seasonable partial defoliation by grazing of grass tillers with 25% to 33% of the leaf material removed during phenological growth between the three and a half new leaf stage and flowering (anthesis) stage (early June to mid July) is beneficial and stimulates compensatory physiological processes, stimulates vegetative reproduction by tillering, and stimulates rhizosphere organism activity (Manske 1999a). The amount of leaf area capable of conducting photosynthesis that remains after partial defoliation is an important factor affecting the quantity of vegetative tiller development and the quantity of replacement herbage biomass produced by the grazed grass tiller. Partial defoliation after the three and a half new leaf stage and before the flower stage that removes 25% of the leaf material stimulates secondary tiller development 38.2% greater than the secondary tiller development from lead tillers that had no defoliation (Manske 2003c) and replacement leaf weight is 40% greater than the weight of the leaf material removed (Manske 2000b). Defoliation that removes 50% of the leaf material after the three and a half new leaf stage and before the flower stage suppresses secondary tiller development 52.9% below the secondary tiller development from lead tillers that had no defoliation (Manske 2003c) and replacement leaf weight is 29.2% less than the weight of the leaf material removed (Manske 2000b).

The greater leaf area and higher levels of nonstructural carbohydrates in grass tillers that have developed three and a half new leaves or more prior to partial defoliation support growth of greater numbers of stimulated vegetative tillers (Coyne et al. 1995), and the resulting development of more secondary tillers increases herbage biomass. Rate of growth of secondary tillers from axillary buds decreases progressively during the growing season as later stimulative defoliation events proceed toward mid July. Early stimulated secondary tillers require less time to reach the three and a half new leaf stage than do later stimulated tillers. The interval between the first grazing period and the return of grazing to a pasture must be lengthened as the growing season progresses to accommodate the increase in time required for leaf development of later stimulated secondary tillers.

Rhizosphere organism activity can be stimulated by increased exudation of carbon compounds (Elliot 1978, Anderson et al. 1981, Curl and Truelove 1986, Whipps 1990). Increased exudation of simple carbon chains from the grass plants' roots into the rhizosphere can be triggered by partial defoliation by grazing of grass tillers (Holland et al. 1996, Hamilton and Frank 2001). Relatively large quantities of carbon can be exuded from healthy grass tiller roots into the rhizosphere during early phenological growth between the three and a half new leaf stage and the flower (anthesis) stage (early June to mid July) when photosynthetically active leaf area is sufficient to export carbohydrates (Manske 1999a; Gorder, Manske, and Stroh 2004) and while the aboveground tiller material consists of a high proportion of nitrogen (crude protein) and a low proportion of structural carbohydrates (fiber) (Manske 1996). A greater quantity of mineral nitrogen is available for plant growth and recovery from defoliation as a result of increased conversion of organic nitrogen from elevated rhizosphere organism activity (Coleman et al. 1983, Ingham et al. 1985, Clarholm 1985, Biondini et al. 1988, Klein et al. 1988, Frederick and Klein 1994, Frank and Groffman 1998, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005). The amount of remobilized nitrogen from the remaining shoot is reduced when a greater amount of mineral nitrogen is available from the media around the root. Mineral nitrogen absorption by the roots greatly increases for several days following partial defoliation of grass tillers (Manske 1999a).

Traditional grazing management practices are not beneficial for grassland ecosystems. The deferred grazing, 6.0-m seasonlong, and 4.5-m seasonlong management strategies are antagonistic to rhizosphere organism activity and biogeochemical processes of the nitrogen cycle and these traditional grazing practices do not stimulate beneficial grass growth processes (Manske 2011b). Traditional grazing practices inhibit the quantity of exudated carbon released through grass roots into the rhizosphere, causing a reduction in rhizosphere biomass and volume, resulting in conversion of organic nitrogen into mineral nitrogen at low rates below the threshold amount of 100 lbs/ac, which prevents full activation of the defoliation resistance mechanisms. The rhizosphere organism biomass and activity and the quantity of available mineral nitrogen decrease by small amounts annually along with proportional decreases in grass density and herbage biomass production. After two, three, or more decades of management of grassland ecosystems with traditional grazing practices, the losses in productivity are substantial. The deferred grazing strategy caused a 70.6% decrease in available mineral nitrogen after 35 years of treatment. The 6.0-m seasonlong grazing strategy caused a 41.9% decrease in mineral nitrogen and a 51.2% decrease in rhizosphere volume after 20 years of seasonlong treatment. The 4.5-m seasonlong grazing strategy caused a 27.7% decrease in mineral nitrogen after 6 years of treatment and caused a 33.7% decrease in rhizosphere volume after 20 years of treatment (Manske 2011b).

The twice-over rotation grazing management strategy is beneficial for grassland ecosystems. The advantageous effects from partial defoliation managed with a twice-over rotation grazing strategy caused a 67.7% increase in available mineral nitrogen after six years of treatment and caused a 122.7% increase in rhizosphere volume after 20 years of treatment (Manske 2011b). Enhancement of the nitrogen cycle in grassland ecosystems that causes an increase in available mineral nitrogen results in greater productivity of herbage, livestock, and wildlife.

Mid and Late Seasonable Defoliation by Grazing

Mid and late seasonable defoliation, after lead tillers have flowered and started to develop seeds (mid July to mid October), is not as beneficial as early seasonable defoliation. Activation by defoliation of the compensatory physiological processes diminishes and removed foliage is not completely replaced. However, mature grass plants can tolerate removal of up to 50% of the aboveground plant material. During middle and late phenological growth stages, the defoliation resistance mechanisms are still triggered by defoliation by grazing of grass tillers (Manske 1999a), but because the aboveground tiller material consists of a high proportion of structural carbohydrates (fiber) and a low quantity of nitrogen (crude protein) (Manske 1996) and leaf senescence has caused decreased photosynthetic and physiological activity with very little or no carbon exudation into the rhizosphere, the compensatory physiological processes are not fully executed. Moreover, the general decreases in soil water level typical of the middle and late portions of the grazing season limit biological processes and rhizosphere organism activity (Curl and Truelove 1986, Bazin et al. 1990).

Deferring the starting date of grazing on native rangeland until after the grass lead tillers have flowered and developed seeds prevents stimulation of the compensatory physiological processes, vegetative reproduction by tillering, and rhizosphere organism activity. The herbage biomass available to grazing livestock on deferred grazing strategies is below the potential quantities (Manske 2000b) and the nutritional quality is below the crude protein requirements of lactating beef cows (Whitman et al. 1951, Manske 1999b) because of leaf senescence and translocation of cell constituents from leaf structures (Langer 1972, Beard 1973, Leopold and Kriedemann 1975). The intended biological purpose of deferred grazing was to increase grass density by promoting seedling development from increased seed stalk quantities and to use trampling by livestock to scatter and plant the resulting seeds. However, grassland ecosystem processes do not function in accordance with the deferred grazing hypothesis.

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 1999a) 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. Sarvis (1941) was unable to determine any improved benefit to grass plant density from reseeding of the grasses after 23 years of deferred grazing treatment. Manske et al. (1988), in a three year study, found that total grass basal cover decreased significantly after one year of deferred grazing treatment. Grassland ecosystems are negatively affected by deferred grazing management from the significant yearly decrease of grass basal cover, grass density, and herbage production, and from the loss of significant energy and resources used for the increased inutile seed production that could have been supplied for increased vegetative tiller production.

Severe defoliation that removes greater than 50% of the leaf material and repeated defoliation with rapid frequency result in insufficient leaf area retained on the tiller for even partial foliage recovery using current photosynthetic assimilates. Tillers with 50% or more of the aboveground leaf material removed reduce root growth, root respiration, and root nutrient absorption (Crider 1955). Root mortality and decomposition begin within 2 days of severe leaf defoliation (Oswalt et al. 1959). Severely defoliated tillers must depend upon stored carbohydrates for replacement leaf growth (Briske and Richards 1995). There is a high biological cost to the tiller when the photosynthetic system needs to be replaced from stored carbohydrates. This implied reduction in efficiency results in reduced root growth, decreased tiller development, and low growth rates causing decreased tiller numbers, reduced total basal area, and reduced quantities of herbage biomass produced (Chapin and Slack 1979, Olson and Richards 1988, Coyne et al. 1995). Continuation of severe defoliation inhibits herbage production further as a result of additional restrictions caused by low levels of stored carbohydrates (Coyne et al. 1995).

Post Seasonable Defoliation by Grazing

Post seasonable defoliation (mid October to March) is not harmful to senescent lead tillers that have produced seeds. However, the lead tillers that did not produce seeds, the secondary tillers, and the fall initiated tillers that will be the future lead tillers of the next growing season are injured by late season defoliation. Secondary tillers with the apical meristem at vegetative status and fall initiated cool-season grass tillers overwinter and resume active growth as lead tillers during early spring of the subsequent growing season. Winter survival and spring regrowth of secondary tillers and fall 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 (Leopold and Kriedemann 1975). The crown, portions of the root system, and some leaf tissue remain active and maintain physiological processes throughout the winter by using stored carbohydrates. Cool-season grasses continue leaf growth at slow rates during the winter. Severe grazing of grass tillers during August to mid October removes sufficient leaf material from secondary tillers and fall tillers to cause inadequate quantities of carbohydrates to be stored. Plants that have low carbohydrate reserves and survive the dormancy period produce tillers with reduced height and weight.

Some tillers with low carbohydrate reserves do not survive until spring. The rate at which plants respire, or use, stored carbohydrates during the 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. When the standing herbage on a grassland is grazed short and most of the snow is blown off, very rapid respiration can occur and deplete carbohydrate reserves before spring, causing tiller death called "winter kill".

At the end of the winter dormancy period, portions of previous years leaves with intact cell walls on surviving tillers regreen with chlorophyll and provide crucial photosynthetic product for new leaf growth (Briske and Richards 1995). New growing leaves draw carbohydrates from these carryover older leaves until maintenance and growth requirements can be met by photosynthetic assimilates produced by the new leaves (Langer 1972, Coyne et al. 1995). Post seasonable defoliation during the fall or winter of viable leaf material on overwintering secondary tillers and fall tillers decreases the quantity of photosynthetic assimilates available to new leaves for growth the following growing season causing a reduction in active leaf growth (Coyne et al. 1995). Defoliation by grazing during fall causes a decrease in plant vigor and a reduction of 28% in leaf height during the succeeding growing season (Goetz 1963, Manske 2003b).

Degraded Grassland Ecosystem Restoration

The primary cause of degradation of prairie ecosystems and the reduction of grassland productivity is management practices that are antagonistic to the ecosystems' living components of grassland plants and soil organisms and that are detrimental to the compensatory physiological processes, the vegetative reproduction mechanisms, and the rhizosphere organism population. Traditional grazing practices of deferred grazing, 6.0-m seasonlong, and 4.5-m seasonlong grazing management, and long-term nondefoliation management are antagonistic to grass tiller biological requirements and to rhizosphere organism biomass and activity (Manske 2011b). Decreases in vegetative reproduction by tillering and reduction of compensatory physiological processes prevents grass tillers from replacing a sufficient proportion of the leaf area removed by defoliation. Low leaf surface reduces the quantity of carbon fixed by photosynthesis. Decreases in rhizosphere organism biomass and activity result in decreased biogeochemical processes of the nitrogen cycle causing reductions in the quantity of organic nitrogen converted into mineral nitrogen (Manske 2007a). Decreases in the quantity of fixed carbon and the quantity of mineral nitrogen in an ecosystem degrade grassland plant communities by causing reductions in grass herbage biomass production and in native plant density, creating larger and more numerous bare spaces between grass plants. These open spaces in the plant communities provide ideal habitat for growth of opportunistic "weedy" plant species that are not dependent on the nitrogen converted by rhizosphere organisms (Manske 2011a). Opportunistic grasses and forbs are not highly competitive and do not increase into plant communities unless openings are created by reductions in native grass densities. Degraded grassland ecosystems have an increasing composition of opportunistic introduced grasses, early succession and weedy forbs, and shrubs (Manske 2007a).

The existence of a shrub component in a grassland plant community is not an ecologically beneficial relationship. Shrubs and grasses are adversarial inhibitive competitors. Grasses and shrubs compete for sunlight, mineral nitrogen, and soil water. Grasses are good competitors for soil water and superior competitors for mineral nitrogen. Shrubs' taller growth makes the plants superior competitors for aboveground resources of sunlight (Kochy and Wilson 2000). Grasses have a 1.4 times greater competitive effect for belowground resources than western snowberry because of their growth forms; grass aboveground biomass is primarily productive photosynthetic leaves, and western snowberry aboveground biomass has a high proportion of unproductive woody stem (Kochy and Wilson 2000). Western snowberry requires six times greater aboveground biomass than the grasses before grass production is decreased as a result of competition from the shrubs (Kochy 1999).

The competitive advantage of healthy grasses for the belowground resources of mineral nitrogen and soil water suppresses western snowberry expansion (Kochy and Wilson 2000). Competition from grasses reduces the growth rates of western snowberry rhizome suckers and causes a relatively high mortality rate of young suckers (Li and Wilson 1998). Antagonistic effects on rhizosphere organism activity from traditional management practices, like deferred grazing and seasonlong grazing, decrease rhizosphere organism activity and reduce the quantity of organic nitrogen converted into mineral nitrogen (Manske 2011b). Reduction of grass plant health and competitiveness follows behind this degradation of biogeochemical processes and the reduction of available mineral nitrogen. As a result of the decrease in grass biomass production and native plant density, grass plants use less resources and larger and more numerous open spaces are created, providing habitat for the growth of opportunistic plant species (Manske 2011a). The belowground resources not consumed by the smaller, less vigorous grasses are taken up by western snowberry plants (Kochy and Wilson 2000). When grass competition for belowground resources is reduced, western snowberry rhizome suckers regain the faster growth rates and higher survival rates (Li and Wilson 1998) resulting in greater shrub stem densities. With increased shrub cover, the competition shifts to the aboveground resources of sunlight, and the western snowberry colonies can expand more rapidly into the weakened grassland (Kochy and Wilson 2000).

Mixed grass prairie ecosystems managed with traditional grazing practices of deferred grazing or seasonlong grazing can be transformed into a degraded grassland infested with shrubs, introduced grasses, and early succession and weedy forbs over a period of about 45 years as a result of antagonistic effects on the rhizosphere organism biomass and activity causing greatly reduced quantities of mineral nitrogen to be converted from soil organic nitrogen (Manske 2011b). The deterioration does not occur at a uniform rate. During the first 20 years, the shrub composition in the plant community does not change much from the original 5% of the land occupied with western snowberry. Over the next 15 years, the shrub cover increases substantially, and during the subsequent 10 years, the western snowberry and associated Kentucky bluegrass colonies expand rapidly and infest greater than 50% of the land area, with a mixture of introduced grasses, early succession and weedy forbs, and depauperated native plants scattered over the remaining area (Manske 2011b).

Restoration of degraded grassland ecosystems can not occur unless the underlying causes are corrected. The observable change in plant composition to greater abundance of nonrhizosphere plants is not a cause but a symptom of ecosystem degradation. The degree of plant species deterioration lags behind the degree of rhizosphere organism activity reduction and the subsequent decrease in the quantity of available mineral nitrogen. The degree of restoration of plant species composition will follow behind the degree of restoration of rhizosphere organism activity and the increase in the quantity of available mineral nitrogen.

The composition of the opportunistic grasses, forbs, and shrubs can be temporarily decreased by prescribed burning, herbicides, and mechanical treatments. However, reduction of the symptoms of ecosystem degradation should not be interpreted as correction of the problems. Herbicides, prescribed burning, and mechanical treatments should not be used as the initial action to recovery because these secondary treatments do not restore degraded grassland ecosystem processes (Manske 2007a, 2011b).

The primary restoration action should be to improve the rhizosphere organism biomass and activity in order to increase the quantity of mineral nitrogen converted from soil organic nitrogen. The next important restoration action is to stimulate the vegetative reproduction mechanisms of the remaining native grass species. Stimulation of the rhizosphere organism activity requires removal of 25% to 33% of the leaf material by defoliation by grazing from grass tillers at phenological growth between the three and a half new leaf stage and the flower (anthesis) stage (early June to mid July), which increases the quantity of carbon exudated from grass roots into the rhizosphere. Full activation of the compensatory physiological processes and the vegetative reproductive processes requires removal of 25% to 33% of the leaf material by defoliation by grazing from grass tillers at phenological growth between the three and a half new leaf stage and the flower stage and also requires the availability of the threshold quantity of mineral nitrogen at 100 pounds per acre or greater (Manske 2009, 2010).

The composition of opportunistic grasses and forbs will decrease as a result of the increasing competition from native grass plants as the available mineral nitrogen increases from the increasing rhizosphere organism biomass and activity and from the increasing vegetative reproduction by tillering the native grass density and herbage biomass production improves. The restoration of ecosystem biogeochemical processes of nutrient cycling is followed by the improvement in plant species composition and the increase in grassland ecosystem productivity.

The composition of the shrubs and a few persistent forbs that increased during the period of ecosystem degradation, however, will not be reduced just by the improved competition from healthy native grasses. Supplemental management practices, such as herbicides, prescribed burning, and mechanical treatments (Manske et al. 2006, Manske 2006), can be implemented as followup treatments to reduce the composition of the problem plants after the rhizosphere organism activity and native grass tiller density have improved substantially.

Implications for Management of Defoliation by Grazing

Productivity on grassland ecosystems depends on the level of rhizosphere organism activity, on the quantity of available mineral nitrogen converted from soil organic nitrogen to be 100 lbs/ac or greater, on the effectiveness of compensatory physiological processes within grass tillers that increase photosynthetic leaf area through increased growth rates, and on the increased secondary tiller production through vegetative reproduction. Management of partial defoliation by grazing that focuses on meeting the biological requirements of the grass plants and of the rhizosphere organisms is beneficial, and enhances the health and productivity of grassland ecosystems.

Biologically effective grazing management activates the defoliation resistance mechanisms. Partial defoliation controlled with the twice-over rotation grazing management strategy that removes 25% to 33% of the leaf material from grass tillers at phenological growth between the three and a half new leaf stage and the flower (anthesis) stage (early June to mid July); stimulates compensatory physiological processes resulting in greater replacement leaf, shoot, and root growth; stimulates vegetative reproduction by tillering resulting in greater grass tiller density and herbage biomass production; and stimulates rhizosphere organism biomass and activity resulting in greater quantities of available mineral nitrogen. The twice-over rotation grazing management system uses three to six native rangeland pastures. Each of the pastures in the rotation is partially defoliated by grazing for 7 to 17 days during the first period, the 45-day interval from 1 June to 15 July when grasses are between the three and a half new leaf stage and flower (anthesis) stage. The length in number of days of the first grazing period on each pasture is the same percentage of 45 days as the percentage of the total season's grazable forage each pasture contributes to the complete system. During the second grazing period when lead tillers are maturing and defoliation by grazing is only moderately beneficial, after mid July and before mid October, each pasture is grazed for double the number of days it was grazed during the first period. Livestock are removed from the native rangeland pastures in mid October.

Restoration of degraded grassland ecosystems and maintenance of healthy functioning grassland ecosystems requires annual partial defoliation by grazing that meets the biological requirements of grass tillers, that enhances rhizosphere organism activity, and that increases the quantity of available mineral nitrogen. Placing defoliation management decision priorities with the living components of the ecosystem is biologically effective, and results in greater forage for livestock, better habitat for wildlife, and more aesthetic open spaces for recreation and sightseeing as sustainable products from biologically managed grassland ecosystems.

Acknowledgment

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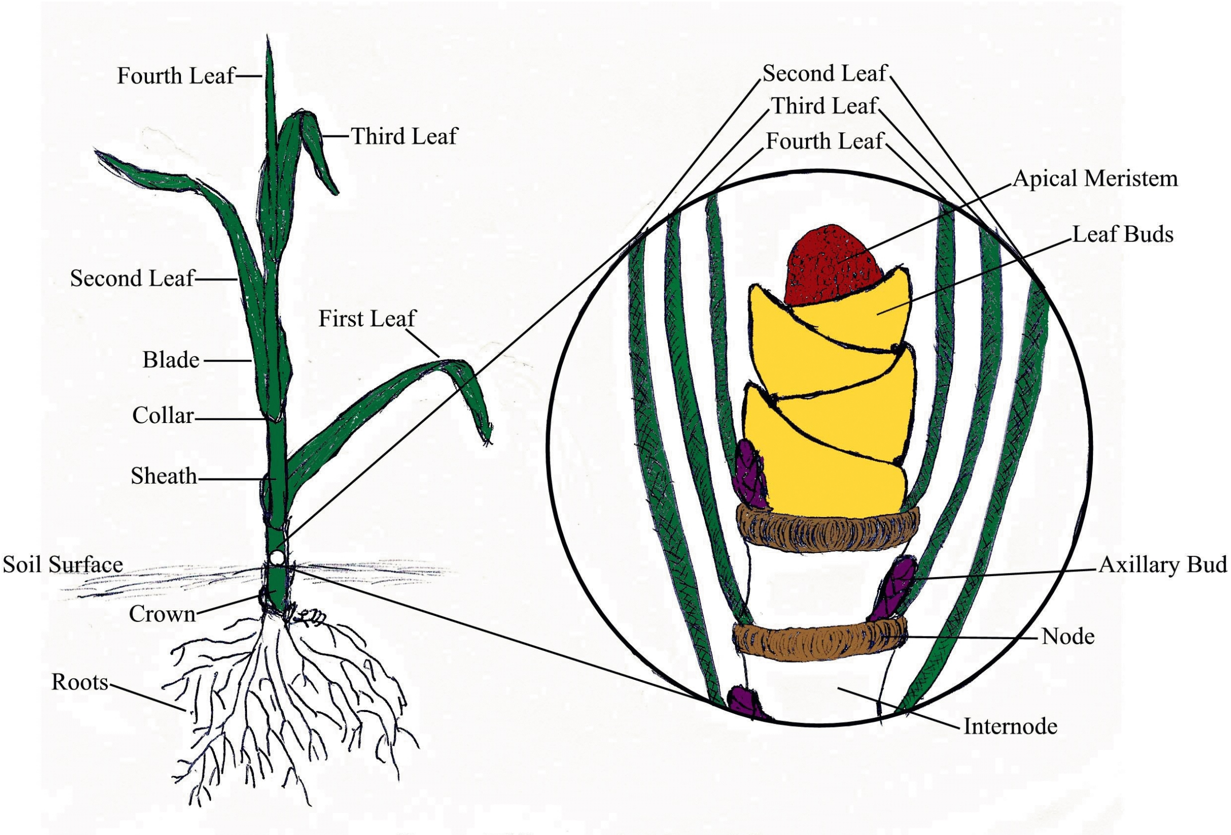
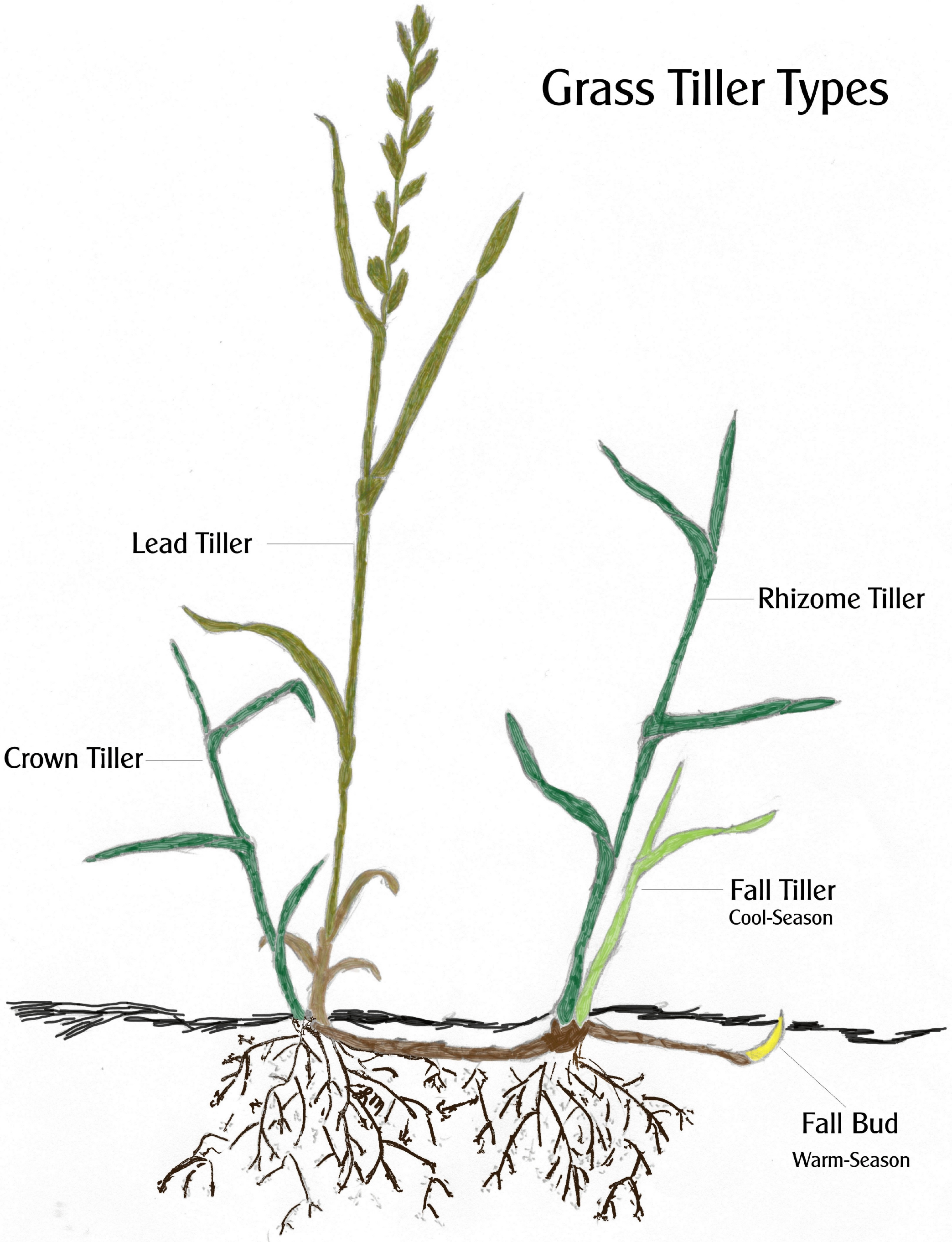


Grass Tiller at 3.5 Leaf Stage



Grass Tiller Types

SYMBIOTIC RHIZOSPHERE ORGANISMS

RHIZOSPHERE STRUCTURE

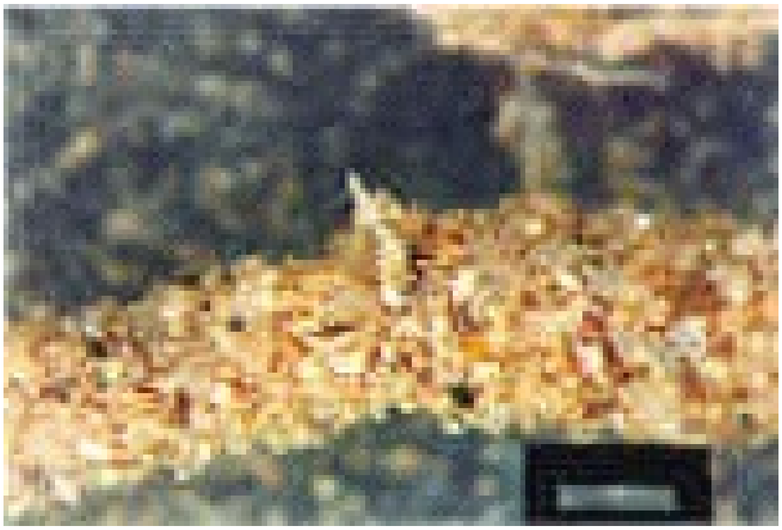


Photo from J. Barrows

Rhizosphere with soil particles bound to plant roots by polysaccharides secreted by mycorrhizal fungi.

MICROFLORA

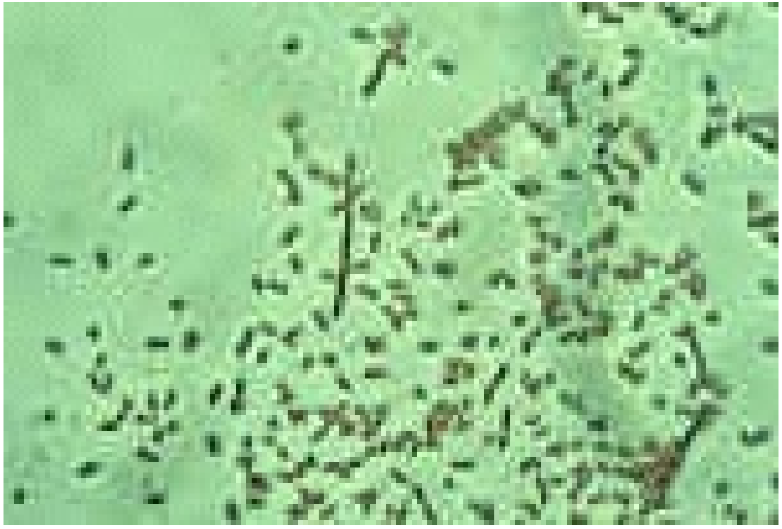


Photo from M.T. Holmes

Bacteria are microscopic single-celled organisms with biomass greater than 2000 pounds per acre.

MYCORRHIZAL FUNGI

ENDOMYCORRHIZAL FUNGI

Photo from R. Campbell

Fungal hyphae strands with bacteria on the surface.

Photo from M. Brundrett

Arbuscules and vesicles of a mycorrhizal fungus within root tissue.

ECTOMYCORRHIZAL FUNGI

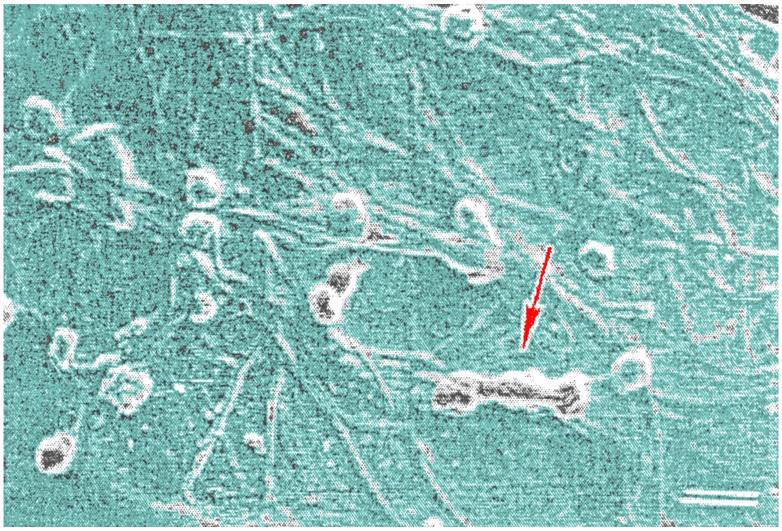


Photo from T.C. Caesar-TonThat

Ectomycorrhizal fungus with extracellular polysaccharides.

MICROFAUNA

PROTOZOA

Photo from J.P. Martin

Amoeba ingesting bacteria.
Protozoa are single-celled microorganisms.

NEMATODES

Photo from H. Garrett

Beneficial nematodes are small nonsegmented worms.

MICROARTHROPODS

SPRINGTAILS

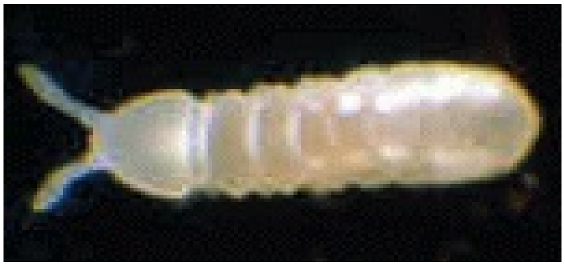


Photo from A.R. Moldenke

Blind fungal-feeding springtail.

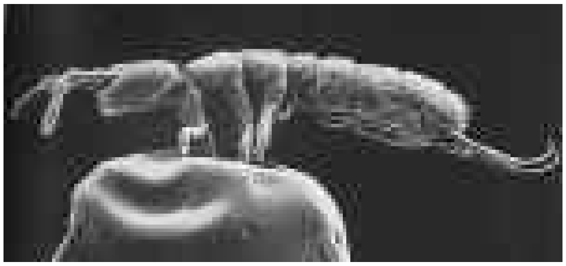


Photo from G. Eisenbeis and W. Wichard

Springtail with furcula released.

Springtails are minute insects.

MITES

Photo from G. Eisenbeis and W. Wichard

Predatory mite.
Mites are small eight-legged arachnids.

Literature Cited

Allen, E.B., and M.F. Allen. 1990. The mediation of competition by mycorrhizae in successional and patchy environments. p. 307-389. *in* J.B. Grace and D. Tilman (eds.). Perspectives on plant competition. Academic Press Inc., San Diego, CA.

Anderson, R.V., D.C. Coleman, C.V. Cole, and E.T. Elliott. 1981. Effect of nematodes *Acrobeloides sp.* and *Mesodiplogaster lheritieri* on substrate utilization and nitrogen and phosphorus mineralization. Ecology 62:549-555.

Atkinson, C.J. 1986. The effect of clipping on net photosynthesis and dark respiration rates of plants from an upland grassland, with reference to carbon partitioning in *Festuca ovina.* Annals of Botany 58:61-72.

Bazin, M.J., P. Markham, E.M. Scott, and J.M. Lynch. 1990. Population dynamics and rhizosphere interactions. p. 99-127. *in* J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

Beard, J.B. 1973. Turfgrass: science and culture. Prentice-Hall, Inc., Englewood Cliffs, NJ.

Belsky, A.J. 1992. Effects of grazing competition, disturbance and fire on species composition and diversity in grassland communities. Journal of Vegetation Science 3:187-200.

Biondini, M., D.A. Klein, and E.F. Redente. 1988. Carbon and nitrogen losses through root exudation by *Agropyron cristatum, A. smithii,* and *Bouteloua gracilis.* Soil Biology and Biochemistry 20:477-482.

Bird, S.B., J.E. Herrick, M.M. Wander, and S.F. Wright. 2002. Spatial heterogeneity of aggregate stability and soil carbon in semi-arid rangeland. Environmental Pollution 116:445-455.

Box, J.E., and L.C. Hammond. 1990. Rhizosphere dynamics. Westview Press, Boulder, CO.

Brand, M.D., and H. Goetz. 1986. Vegetation of exclosures in southwestern North Dakota. Journal of Range Management 39:434-437.

Branson, F.A. 1953. Two new factors affecting resistance of grasses to grazing. Journal of Range Management 6:165-171.

Briske, D.D. 1991. Developmental morphology and physiology of grasses. p. 85-108. *in* R.K. Heitschmidt and J.W. Stuth (eds.). Grazing management: an ecological perspective. Timber Press, Portland, OR.

Briske, D.D., and J.H. Richards. 1994. Physiological responses of individual plants to grazing: current status and ecological significance. p. 147-176. *in* M. Vavra, W.A. Laycock, and R.D. Pieper (eds.). Ecological implications of livestock herbivory in the west. Society for Range Management, Denver, CO.

Briske, D.D., and J.H. Richards. 1995. Plant response to defoliation: a physiological, morphological, and demographic evaluation. p. 635-710. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Burrows, R.L., and F.L. Pfleger. 2002. Arbuscular mycorrhizal fungi respond to increasing plant diversity. Canadian Journal of Botany 80:120-130.

Butler, J.L., and D.D. Briske. 1988. Population structure and tiller demography of the bunch grass *Schizachyrium scoparium* in response to herbivory. Oikos 51:306-312.

Caesar-TonThat, T.C., and V. Cochran. 2000. Soil aggregate stabilization by a saprophytic lignin-decomposing basidiomycete fungus. I. Microbiological aspects. Biology and Fertility of Soils 32:374-380.

Caesar-TonThat, T.C., W. Shelver, R.G. Thorn, and V.L. Cochran. 2001a. Generation of antibodies for soil-aggregating basidiomycete detection to determine soil quality. Applied Soil Ecology 18:99-116.

Caesar-TonThat, T.C., D.H. Branson, J.D. Reeder, and L.L. Manske. 2001b. Soil-aggregating basidiomycetes in the rhizosphere of grasses under two grazing management systems. Poster. American Society of Agronomy Annual Meeting. Charlotte, NC.

Caesar-TonThat, T.C. 2002. Soil binding properties of mucilage produced by a basidiomycete fungus in a model system. Mycological Research 106:930-937.

Campbell, J.B. 1952. Farming range pastures. Journal of Range Management 5:252-258.

Campbell, R., and M.P. Greaves. 1990. Anatomy and community structure of the rhizosphere. p. 11-34. *in* J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

Chapin, S.F., and M. Slack. 1979. Effect of defoliation upon root growth, phosphate absorption and respiration in nutrient-limited tundra graminoids. Oecologia 42:67-79.

Chapman, G.P., and W.E. Peat. 1992. An introduction to the grasses. C.A.B. International, Wallingford, UK. 111p.

Chapman, G.P. 1996. The biology of grasses. C.A.B. International, Wallingford, UK. 273p.

Clarholm, M. 1985. Interactions of bacteria, protozoa, and plants leading to mineralization of soil nitrogen. Soil Biology and Biochemistry 17:181-187.

Coleman, D.C., C.P.P. Reid, and C.V. Cole. 1983. Biological strategies of nutrient cycling in soil ecosystems. Advances in Ecological Research 13:1-55.

Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995. Carbon and nitrogen dynamics in range plants. p. 59-167. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Crider, F.J. 1955. Root-growth stoppage resulting from defoliation of grass. USDA Technical Bulletin 1102.

Curl, E.A., and B. Truelove. 1986. The rhizosphere. Springer-Verlag, New York, NY.

Dahl, B.E., and D.N. Hyder. 1977. Developmental morphology and management implications. p. 257-290. *in* R.E. Sosebee (ed.). Rangeland plant physiology. Range Science Series No. 4. Society for Range Management, Denver, CO.

Dahl, B.E. 1995. Developmental morphology of plants. p. 22-58. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Driver, J.D., W.E. Holben, and M.C. Rillig. 2005. Characterization of glomalin as a hyphal wall component of arbuscular mycorrhizal fungi. Soil Biology and Biochemistry 37:101-106.

Elliot, E.T. 1978. Carbon, nitrogen and phosphorus transformations in gnotobiotic soil microcosms. M.S. Thesis. Colorado State University, Ft. Collins, CO.

Esau, K. 1960. Anatomy of seed plants. Wiley and Sons, New York, NY.

Evans, M.W., and F.O. Grover. 1940. Developmental morphology of the growing point of the shoot and the inflorescence in grasses. Journal of Agricultural Research 61:481-520.

Frank, A.B., J.D. Berdahl, and J.F. Karn. 1997. Phyllochron development in cool-season grasses. XVIII International Grassland Congress Poster.

Frank, A.B. 1996. Evaluating grass development for grazing management. Rangelands 18:106-109.

Frank, D.A., and P.M. Groffman. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. Ecology 79:2229-2241.

Frederick, B.A., and D.A. Klein. 1994. Nitrogen effects on rhizosphere processes of range grasses from different successional seres. Plant and Soil 161:241-250.

Goetz, H. 1963. Growth and development of native range plants in the mixed prairie of western North Dakota. M. S. Thesis, North Dakota State University, Fargo, ND. 165p.

Gorder, M.M., L.L. Manske, and T.L. Stroh. 2004. Grazing treatment effects on vegetative tillering and soil rhizospheres of western wheatgrass. NDSU Dickinson Research Extension Center. Range Research Report DREC 04-1056. Dickinson, ND. 13p.

Grant, S.A., G.T. Barthram, L. Torvell, J. King, and H.K. Smith. 1983. Sward management, lamina turnover and tiller population density in continuously stocked *Lolium perenne*-dominated swards. Grass and Forage Science 38:333-344.

Hamilton, E.W., and D.A. Frank. 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82:2397-2402.

Harley, J.L., and S.E. Smith. 1983. Mycorrhizal symbiosis. Academic Press, New York, NY.

Heady, H.F. 1975. Rangeland management. McGraw-Hill Book Company, New York, NY.

Holland, J.N., W. Cheng, and D.A. Crossley, Jr. 1996. Herbivore-induced changes in plant carbon allocation: assessment of below-ground C fluxes using carbon-14. Oecologia 107:87-94.

Hyder, D.N. 1974. Morphogenesis and management of perennial grasses in the U.S. p. 89-98. *in* Plant morphogenesis as the basis for scientific management for range resources. USDA Miscellaneous Publication 1271.

Ingham, R.E., J.A. Trofymow, E.R. Ingham, and D.C. Coleman. 1985. Interactions of bacteria, fungi, and the nemotode grazers: effects of nutrient cycling and plant growth. Ecological Monographs 55:119-140.

Klein, D.A., B.A. Frederick, M. Biondini, and M.J. Trlica. 1988. Rhizosphere microorganism effects on soluble amino acids, sugars, and organic acids in the root zone of *Agropyron cristatum, A. smithii,* and *Bouteloua gracilis*. Plant and Soil 110:19-25.

Kochy, M., and S.D. Wilson. 2000. Competitive effects of shrubs and grasses in prairie. Oikos 91:385-395.

Kochy, M. 1999. Grass-tree interactions in western Canada. Ph.D. Dissertation. University of Regina. Regina, Saskatchewan, Canada.

Koide, R.T. 1993. Physiology of the mycorrhizal plant. p. 33-54. *in* D.S. Ingram and P.H. Williams (eds.). Mycorrhiza synthesis. Academic Press, London, UK.

Langer, R.H.M. 1956. Growth and nutrition of timothy (*Phleum pratense).* I. The life history of individual tillers. Annals of Applied Biology 44:166-187.

Langer, R.H.M. 1963. Tillering in herbage grasses. Herbage Abstracts 33:141-148.

Langer, R.H.M. 1972. How grasses grow. Edward Arnold, London, Great Britain.

Leopold, A.C., and P.E. Kriedemann. 1975. Plant growth and development. McGraw-Hill Book Co., New York, NY.

Li, X., and S.D. Wilson. 1998. Facilitation among woody plants establishing in an old field. Ecology 79:2694-2705.

Manske, L.L., W.T. Barker, and M.E. Biondini. 1988. Effects of grazing management treatments on grassland plant communities and prairie grouse habitat. USDA Forest Service. General Technical Report RM-159. p. 58-72.

Manske, L.L. and T.C. Caesar-TonThat. 2003. Increasing rhizosphere fungi and improving soil quality with biologically effective grazing management. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 03-3025. Dickinson, ND. 6p.

Manske, L.L., S.A., Schneider, and A.M. Kraus. 2006. Management of western snowberry aka wolfberry and buckbrush. NDSU Dickinson Research Extension Center. Rangeland Research Extension Program 4009. Dickinson, ND. 107p.

Manske, L.L. 1994. Problems to consider when implementing grazing management practices in the Northern Great Plains. NDSU Dickinson Research Extension Center. Range Management Report DREC 94-1005. Dickinson, ND. 11p.

Manske, L.L. 1996. Adaptive tolerance mechanisms in grass plants. p. 97-99. *in* Z. Abouguendia (ed.). Total ranch management in the Northern Great Plains. Grazing and Pasture Technology Program, Saskatchewan Agriculture and Food. Regina, Saskatchewan, Canada.

Manske, L.L. 1999a. Can native prairie be sustained under livestock grazing? p. 99-108. *in* J. Thorpe, T.A. Steeves, and M. Gollop (eds.). Proceedings of the Fifth Prairie Conservation and Endangered Species Conference. Provincial Museum of Alberta. Natural History Occasional Paper No. 24. Edmonton, Alberta, Canada.

Manske, L.L. 1999b. Annual nutritional quality curves for graminoids in the Northern Great Plains. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 99-3014. Dickinson, ND. 14p.

Manske, L.L. 2000a. Management of Northern Great Plains prairie based on biological requirements of the plants. NDSU Dickinson Research Extension Center. Range Science Report DREC 00-1028. Dickinson, ND. 12p.

Manske, L.L. 2000b. Grazing before grass is ready. NDSU Dickinson Research Extension Center. Range Management Report DREC 00-1032. Dickinson, ND. 6p.

Manske, L.L. 2003a. Effects from long-term nongrazing. NDSU Dickinson Research Extension Center. Range Management Report DREC 03-1011b. Dickinson, ND. 8p.

Manske, L.L. 2003b. Effects of fall grazing on grass-leaf height. NDSU Dickinson Research Extension Center. Range Management Report DREC 03-1031b. Dickinson, ND. 7p.

Manske, L.L. 2003c. Effects of grazing management treatments on rangeland vegetation. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 03-3027. Dickinson, ND. 6p.

Manske, L.L. 2006. Chemical management of silver sagebrush. NDSU Dickinson Research Extension Center. Range Research Report DREC 06-1065. Dickinson, ND. 38p.

Manske, L.L. 2007. Effects on vegetation, endomycorrhizal fungi, and soil mineral nitrogen from prescribed burning treatments repeated every-other-year in mixed grass prairie invaded by western snowberry. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 07-3044. Dickinson, ND. 19p.

Manske, L.L. 2009. Grass plant responses to defoliation. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1074. Dickinson, ND. 47p.

Manske, L.L. 2010. Evaluation of the defoliation resistance mechanisms influence on vegetative tiller initiation and tiller density. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1076. Dickinson, ND. 13p.

Manske, L.L. 2011a. Restoration of degraded prairie ecosystems. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 11-3045b. Dickinson, ND. 8p.

Manske, L.L. 2011b. Grazing and burning treatment effects on soil mineral nitrogen and rhizosphere volume. NDSU Dickinson Research Extension Center. Range Research Report DREC 11-1066c. Dickinson, ND. 15p.

Marschner, H., and B. Dell. 1994. Nutrient uptake in mycorrhizal symbiosis. Plant and Soil 159:89-102.

Marschner, H. 1992. Nutrient dynamics at the soil-root interface (Rhizosphere). p. 3-12. *in* D.J. Read, D.H. Lewis, A.H. Fitter, and I.J. Alexander (eds.). Mycorrhizas in ecosystems. C.A.B. International, Wallingford, U.K.

McMillan, C. 1957. Nature of the plant community. III. Flowering behavior within two grassland communities under reciprocal transplanting. American Journal of Botany 44:144-153.

McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist 113:691-703.

McNaughton, S.J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329-336.

Millard, P., R.J. Thomas, and S.T. Buckland. 1990. Nitrogen supply affects the remobilization of nitrogen for the growth of defoliation *Lolium perenne* L.J. Experimental Botany 41:941-947.

Moorman, T., and F.B. Reeves. 1979. The role of endomycorrhizae in revegetation practices in the semi-arid west. II. A bioassay to determine the effect of land disturbance on endomycorrhizal populations. American Journal of Botany 66:14-18.

Moser, L.E. 1977. Carbohydrate translocation in range plants. p. 47-71 *in* R.E. Sosebee (ed.). Rangeland plant physiology. Range Science Series No. 4. Society for Range Management, Denver, CO.

Mueller, R.J., and J.H. Richards. 1986. Morphological analysis of tillering in *Agropyron spicatum* and *Agropyron desertorum.* Annals of Botany 58:911-921.

Murphy, J.S., and D.D. Briske. 1992. Regulation of tillering by apical dominance: chronology, interpretive value, and current perspectives. Journal of Range Management 45:419-429.

Olson, B.E., and J.H. Richards. 1988. Spatial arrangement of tiller replacement in *Agropyron desertorum* following grazing. Oecologia 76:7-10.

Oswalt, D.L., A.R. Bertrand, and M.R. Teel. 1959. Influence of nitrogen fertilization and clipping on grass roots. Soil Science Society Proceedings 23:228-230.

Ourry, A., J. Boucaud, and J. Salette. 1990. Partitioning and remobilization of nitrogen during regrowth in nitrogen-deficient ryegrass. Crop Science 30:1251-1254.

Rechenthin, C.A. 1956. Elementary morphology of grass growth and how it affects utilization. Journal of Range Management 9:167-170.

Richards, J.H., and M.M. Caldwell. 1985. Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: a field study with *Agropyron* species. Journal of Applied Ecology 22:907-920.

Richards, J.H., R.J. Mueller, and J.J. Mott. 1988. Tillering in tussock grasses in relation to defoliation and apical bud removal. Annals of Botany 62:173-179.

Rillig, M.C., S.F. Wright, and V.T. Eviner. 2002. The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. Plant and Soil 238:325-333.

Roberts, R.M. 1939. Further studies of the effects of temperature and other environmental factors upon the photoperiodic response of plants. Journal of Agricultural Research 59:699-709.

Rogler, G.A., R.J. Lorenz, and H.M. Schaaf. 1962. Progress with grass. North Dakota Agricultural Experiment Station. Bulletin 439. 15p.

Ryle, G.J., and C.E. Powell. 1975. Defoliation and regrowth in the graminaceous plant: the role of current assimilate. Annals of Botany 39:297-310.

Sarvis, J.T. 1941. Grazing investigations on the Northern Great Plains. North Dakota Agricultural Experiment Station. Bulletin 308. Fargo, ND.

Smith, S.E., and D.J. Read. 1997. Mycorrhizal symbiosis. Academic Press, San Diego, CA.

Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58:3-15.

Vogel, W.G., and A.J. Bjugstad. 1968. Effects of clipping on yield and tillering of little bluestem, big bluestem, and Indiangrass. Journal of Range Management 21:136-140.

Weier, T.E., C.R. Stocking, and M.G. Barbour. 1974. Botany: an introduction to plant biology. John Wiley and Sons, New York, NY.

Whipps, J.M. 1990. Carbon economy. p. 59-97. *in* J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

Whitman, W.C., D.W. Bolin, E.W. Klosterman, H.J. Klostermann, K.D. Ford, L. Moomaw, D.G. Hoag, and M.L. Buchanan. 1951. Carotene, protein, and phosphorus in range and tame grasses of western North Dakota. North Dakota Agricultural Experiment Station. Bulletin 370. Fargo, ND. 55p.

Whitman, W.C. 1974. Influence of grazing on the microclimate of mixed grass prairie. p. 207-218. *in* Plant Morphogenesis as the basis for scientific management of range resources. USDA Miscellaneous Publication 1271.

Wilson, A.M., and D.D. Briske. 1979. Seminal and adventitious root growth of blue grama seedlings on the central plains. Journal of Range Management 32:209-213.

Ectomycorrhizal Basidiomycete Fungi Detected in Rhizospheres of Mixed Grass Prairie Grasses

Report DREC 07-3047

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Ectomycorrhizal basidiomycete fungi have the ability to aggregate and stabilize soil particles improving soil quality (Caesar-TonThat and Cochran 2000). Soil aggregating tests indicated that basidiomycete fungi from the russuloid clade form water-stable aggregates of soil particles and are very effective soil stabilizers (Caesar-TonThat et al. 2001a).

Apparent changes in soil structure and quality have been observed on native rangeland pastures after a few years of being managed with the twice-over rotation grazing management strategy; watershed harvest dams fail to fill because of a decrease in water runoff, and grass plant roots grow to greater depths of around 12 to 24 inches deeper than with previous grazing management practices. The predominantly clayey soils on a McKenzie county, ND ranch changed from a rooting depth and water holding soil profile of 2 to 3 inches to an aggregated soil of 18 to 24 inches in depth after seven years of management with the twice-over rotation system. A project was conducted to determine if ectomycorrhizal fungi were the cause of the observed improvements in soil characteristics on the twice-over rotation managed pastures.

Procedures

This project was conducted on the NDSU Dickinson Research Extension Center ranch located in Dunn county in western North Dakota, USA, at 47° 14' north latitude, 102° 50' west longitude. The region has a typical continental climate (Manske 2007). Soils are primarily Typic Haploborolls developed on sedimentary deposits. Native vegetation is the Wheatgrass-Needlegrass Type (Barker and Whitman 1988) of the mixed grass prairie.

Soil samples with grass roots were collected during the field seasons of 1999 and 2000 from sandy and silty ecological sites of pastures managed with 6.0-m seasonlong and twice-over rotation grazing management strategies. Each of the grazing treatments had two replications. Livestock on the 6.0-m seasonlong management treatment grazed one native rangeland pasture for 6.0 months (183 days) from mid May until mid November. Livestock on the twice-over rotation management treatment followed a double rotation sequence through three native rangeland pastures for 4.5 months (135 days) from early June until mid October.

Soil samples were analyzed for the presence of ectomycorrhizal basidiomycete fungi by TheCan Caesar-TonThat PhD, Soil Microbiologist, USDA, Agricultural Research Service, Sidney, MT. The soil field cores were divided into 3 layers: layer 1, 0-1 inch (0-2.5 cm); layer 2, 1-3 inches (2.5-7.5 cm); and layer 3, 3-5 inches (7.5-12.5 cm) in depth. Roots with 1 mm diameter and greater were delicately removed from each soil layer, placed on a 2 mm sieve, and immersed in water for 5 minutes with continuous agitation. The soil adhering to the roots was defined as water stable rhizosphere soil (Caesar-TonThat et al. 2001b).

An immunological technique, Enzyme-Linked Immunosorbent Assay (ELISA), was developed for the detection and quantification of ectomycorrhizal basidiomycete fungi (Caesar-TonThat and Cochran 2000, Caesar-TonThat et al. 2001a). Polyclonal antibodies were raised against a soil aggregating basidiomycete fungus (BB1) isolated from plant residue of a cornfield in eastern Montana (Caesar-TonThat and Cochran 2000). These antibodies cross-reacted specifically with fungi from the russuloid clade of the homobasidiomycetes (Caesar-TonThat et al. 2001a). Antigens derived from rhizosphere soil were prepared in carbonate buffer (pH 9.6) and were loaded in microtiter plate wells, followed by incubation overnight at 55° C. After three washings with PBS-Tween 20 buffer, polyclonal sera were added to each well. After 90 minutes of incubation at 22° C, the plates were washed, then incubated for 60 minutes at 22° C with horseradish peroxidase-conjugated goat anti-rabbit polyspecific immunoglobulins. The substrate consisted of a solution of 3, 3', 5, 5' tetramethylbenzidine and hydrogen peroxide. Absorbance was read at the dual wavelength of 450 nm. All samples were processed in triplicate. Results were statistically analyzed using ANOVA models (Caesar-TonThat et al. 2001b).

Results

Absorbance readings (Caesar-TonThat et al. 2001b) for the detection of antigens in the rhizosphere soil adhering to roots of mixed grass prairie grasses determined the presence of ectomycorrhizal basidiomycete fungi from the Homobasidiomycete class and the Russuloid clade. These ectomycorrhizal fungi were previously unknown from the mixed grass prairie. The absorbance values were significantly greater on the twice-over rotation treatment than on the seasonlong treatment for all 3 layers of the sandy soils and for layer 2 of the silty soils. No significant difference was detected in layers 1 and 3 of the silty soils (Caesar-TonThat et al. 2001b).

Discussion

Fungi in the Homobasidiomycete class and the Russuloid clade form ectomycorrhizae; the hyphae do not enter tissue of the host plant but develop a sheath around the root (Harley and Smith 1983). Rhizosphere organism growth and activity are limited by a deficiency of carbon (energy) (Curl and Truelove 1986). Enhancement of the development of ectomycorrhizal fungi in rhizospheres of mixed grass prairie grasses occurs as a result of the beneficial effects from defoliation by grazing controlled with the twice-over rotation grazing management strategy. Partial defoliation by grazing of grass tillers with 25% to 33% of the leaf material removed during phenological growth between the three and a half new leaf stage and the flowering (anthesis) stage (early June to mid July) causes exudation of greater quantities of carbon compounds through grass plant roots into the rhizosphere stimulating organism activity (Manske 1999). Active basidiomycete fungi form water-stable aggregates in soil that are water permeable but not water soluable by secreting large amounts of insoluable extracellular polysaccharides that have adhesive qualities (Caesar-TonThat et al. 2001b). Adhesive polysaccharides act as binding agents for soil particles, causing aggregation of soil (Caesar-TonThat 2002) that range from about the size of air rifle pellets to the size of large marbles. Increases in soil aggregation enlarges soil pore size and improves distribution and stabilization of soil particles. These improvements in soil quality cause increases in soil oxygenation, increases in water infiltration, and decreases in erodibility (Caesar-TonThat and Cochran 2000, Caesar-TonThat et al. 2001a, Caesar-TonThat et al. 2001b, Caesar-TonThat et al. 2002, Manske and Caesar-TonThat 2003). Increased soil aggregation contributes to improvement of grassland ecosystem health and productivity.

Importance

Detection of ectomycorrhizal basidiomycete fungi in the rhizosphere of grass plants in the mixed grass prairie is an important scientific discovery. Very few herbaceous species are known to form ectomycorrhizae on their roots (Harley and Smith 1983). Ectomycorrhizal fungi are slow growing and are limited almost exclusively to associations with woody perennial plants (Harley and Smith 1983).

Substantiation that defoliation by grazing controlled with the twice-over rotation grazing management strategy beneficially stimulates activity of ectomycorrhizal fungi that results in increased soil aggregation and thereby improving the quality of soil is a significant development for biologically effective grazing management of grassland ecosystems.

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Literature Cited

Barker, W.T., and W.C. Whitman. 1988. Vegetation of the Northern Great Plains. Rangelands 10:266-272.

Caesar-TonThat, T.C., and V. Cochran. 2000. Soil aggregate stabilization by a saprophytic lignin-decomposing basidiomycete fungus. I. Microbiological aspects. Biology and Fertility of Soils 32:374-380.

Caesar-TonThat, T.C., W. Shelver, R.G. Thorn, and V.L. Cochran. 2001a. Generation of antibodies for soil-aggregating basidiomycete detection to determine soil quality. Applied Soil Ecology 18:99-116.

Caesar-TonThat, T.C., D.H. Branson, J.D. Reeder, and L.L. Manske. 2001b. Soil-aggregating basidiomycetes in the rhizosphere of grasses under two grazing management systems. Poster. American Society of Agronomy Annual Meeting. Charlotte, NC.

Caesar-TonThat, T.C. 2002. Soil binding properties of mucilage produced by a basidiomycete fungus in a model system. Mycological Research 106:930-937.

Curl, E.A., and B. Truelove. 1986. The rhizosphere. Springer-Verlag, New York, NY.

Harley, J.L., and S.E. Smith. 1983. Mycorrhizal symbiosis. Academic Press, New York, NY.

Manske, L.L. and T.C. Caesar-TonThat. 2003. Increasing rhizosphere fungi and improving soil quality with biologically effective grazing management. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 03-3025. Dickinson, ND. 6p.

Manske, L.L. 1999. Can native prairie be sustained under livestock grazing? p. 99-108. *in* J. Thorpe, T.A. Steeves, and M. Gollop (eds.). Proceedings of the Fifth Prairie Conservation and Endangered Species Conference. Provincial Museum of Alberta. Natural History Occasional Paper No. 24. Edmonton, Alberta, Canada.

Manske, L.L. 2007. Ombrothermic interpretation of range plant water deficiency from temperature and precipitation data collected at the Ranch Headquarters of the Dickinson Research Extension Center in western North Dakota, 1982-2006. NDSU Dickinson Research Extension Center. Range Research Report DREC 07-1019j. Dickinson, ND. 17p.

Biogeochemical Model to Improve Soil Quality

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Soil quality and soil production capacity of the worlds renewable natural resources, which are the rangelands, grasslands, and croplands, have severely decreased as a result of diminished ecological processes (Bloem et al. 2006).

These renewable natural resources are no longer able to maintain current production at potential levels as a result of the management caused deterioration of the ecosystem processes. The primary reason for this decline in resource productivity is that management of renewable natural resources has traditionally been conducted from the perspective of the "use" of the resource. The value of a resource has been determined by the quantity of product removed. This shortsighted management has not considered renewable resources as complete functioning ecosystems and consequently has diminished the biogeochemical processes, decreased the soil microorganism biomass, and caused the loss or removal of greater quantities of essential elements than the amount replaced annually (Manske 2008).

Soils with low quality generally have low organic matter content, low quantities of essential elements, low microorganism biomass, low biogeochemical activity, low aggregation and poor structure, reduced pore spaces, low aeration, and low water infiltration (Manske 2012b).

The primary stages for restoration of low quality soils requires improvement of the biogeochemical processes, increases of the soil microorganisms biomass, and replacement of lost or removed essential elements. Vital improvement in soil quality of renewable resources has been impeded because of the unavailability of a thorough description of the ecological processes in high quality soils (Manske 2013b).

A description of the ecological processes in managed high quality cropland soils has not yet been produced (Bloem et al. 2006). However, the biogeochemical processes of biologically managed high quality prairie soils have been described (Manske 2013b). Rangeland, grassland, and most cropland soils were transformed from prairie soils. The biogeochemical processes in renewable resources soils should be analogous to the biogeochemical processes in prairie soils. The described ecological processes in prairie soils can realistically provide a functional prototype from which to use as procedural guidelines for soil quality improvement of the other renewable natural resources (Manske 2013b).

Management that will improve soil quality must consider renewable natural resources as complex ecosystems consisting of numerous interactive biotic (living) and abiotic (nonliving) components. The biotic components are the plants, soil microorganisms, and large organisms (insects, wildlife, and livestock) that have biological and physiological requirements. The abiotic components include the major and minor essential elements that have transformable characteristics between organic and inorganic forms through biogeochemical processes, and also includes the abiotic radiant energy from the sun. Soil ecosystems are functioning units of coacting biotic organisms interacting with the abiotic components and the environmental conditions. If any of the numerous interactive biogeochemical processes are not functioning at potential level, the ecosystem does not produce at potential level (Manske 2012a).

Renewable natural resource ecosystems are open systems with biological, geological, chemical, and atmospheric pathways that transfer the major essential elements into and out of the ecosystem. The major essential elements are carbon, hydrogen, nitrogen, and oxygen and they have separate but closely linked biogeochemical cycles that transform the elements between organic and inorganic forms. Light is radiant energy from the sun, it is necessary for photosynthesis, and it is the initial source of energy for all trophic levels in the food web of an ecosystem (Manske 2013a).

The minor essential elements consist of seven macrominerals and ten microminerals that are required by most living organisms (Manske 2001). The minor elements have biogeochemical cycles or parts of cycles that transform the elements between organic and inorganic forms while they are within an ecosystem. There are numerous pathways that transfer minor essential elements out of an ecosystem. However, there are no readily available natural pathways that can transfer minor essential elements into an ecosystem. After a macromineral or a micromineral has been completely depleted from a renewable natural resource ecosystem, that soil is deficient of that minor essential element.

Renewable resource ecosystems that have greater output than input of essential elements are deteriorating and are not sustainable. Ecosystems that are managed to have greater natural input than output of essential elements have high quality soil and are sustainable (Manske 2012a).

The working model that improves soil quality of a renewable natural resource ecosystem follows the management of a grazed grassland. The management strategies must meet the biological and physiological requirements of the biotic components, stimulate the biogeochemical processes that cycle the abiotic components to function at potential capacity, and replenish the essential elements through ecosystem processes at the same or greater quantities at which the elements were lost or removed from the ecosystem (Manske 2008).

Perennial grass plants on a grazed grassland produce twice the leaf biomass needed to synthesize the compounds used in growth and physiological processes. About 67% of the annual perennial grass biomass is produced belowground and about 33% is produced aboveground. About 50% of the aboveground biomass is expendable by the plant. About 50% of the expendable leaf material is removed as senescent leaves that are broken from the plant and fall to the ground, or as leaf material consumed by insects and wildlife. About 50% of the expendable leaf material, or 25% of the aboveground biomass, is consumed by grazing livestock (Manske 2012a).

Perennial grass leaf material consists of digestible nutrients and nondigestible structural components. All of the nondigestible dry matter consumed by grazing livestock is deposited on the ground as manure in a couple of days. Most of the nutrients consumed and used by livestock for maintenance are returned to the ecosystem in the feces and urine. About 15% of the nutrients contained in the consumed leaf material is extracted by stocker heifers and steers and retained for growth. About 30% of the nutrients contained in the consumed leaf material is extracted by lactating cows, with a portion retained by the cow for production, and the remainder of the extracted nutrients passed to her calf for growth (Russelle 1992, Gibson 2009).

None of the aboveground and belowground dry matter biomass produced during the growing season is removed by livestock from the grazingland ecosystem. All of the essential elements contained in the belowground biomass stay in the ecosystem. The essential elements contained in the nonconsumed aboveground biomass stay in the ecosystem. Livestock consume about 25% of the aboveground biomass. About 85% of the essential elements consumed by livestock are returned to the ecosystem in the feces and urine. Nearly all of the essential elements used in the annual production of plant herbage biomass, soil organism biomass, insect biomass, wildlife biomass, and livestock biomass are retained and recycled within the ecosystem (Manske 2013a).

The small quantity of major essential elements that are lost or removed annually from a renewable natural resource ecosystem can be replenished at equal or greater amounts by capturing input major essential elements from the surrounding environment through ecosystem processes associated with active plants or soil microorganisms (Manske 2013a).

Atmospheric carbon dioxide is the ecosystem input source for carbon. The carbon dioxide is fixed with hydrogen from soil water during the plant process of photosynthesis which converts energy from sunlight into chemical energy and assimilates simple carbohydrates (Manske 2013c).

Soil water is infiltrated precipitation water and is the ecosystem input source for hydrogen. Soil water is absorbed through the roots and distributed throughout the plant within the xylem vascular tissue (Manske 2013c).

Wet deposition of nitrogen oxides following lightning discharge is the ecosystem input source for nitrogen at an average rate of 5 to 6 pounds per acre per year. The source of nitrogen for plant growth is the mineral nitrogen converted from soil organic nitrogen by soil microorganisms (Manske 2013c). The greater the soil microorganism biomass, the greater the quantity of available soil mineral nitrogen.

Atmospheric and soil elemental oxides are the ecosystem input sources for oxygen. The oxygen biogeochemical cycle is closely linked to the carbon cycle and the water cycle (Manske 2013c).

Radiant light from the sun is the ecosystem input source for energy (Manske 2013c). Solar energy is the only energy source that powers biogeochemical processes in renewable natural resource ecosystems.

Energy flow within an ecosystem includes three biogeochemical cycles, the carbon, hydrogen, and oxygen cycles. Photosynthesis is the process that captures energy. Respiration is the process that releases energy (Manske 2013a).

Nitrogen flow within an ecosystem includes four biogeochemical cycles, the nitrogen, oxygen, carbon, and hydrogen cycles. Immobilization is the process that changes nitrogen from inorganic forms to organic forms, primarily nucleic acids and proteins. Mineralization is the process that changes nitrogen from organic forms to inorganic forms, primarily mineral nitrogen as nitrate and ammonium. A great soil microorganism biomass is required for adequate nitrogen flow in renewable natural resource ecosystems (Manske 2013a).

Decomposition of organic matter within an ecosystem includes all of the biogeochemical cycles. Decomposition is the process that changes complex organic matter into compounds and then into the essential elemental forms by soil microorganisms. The large soil microorganism biomass required for decomposition of an ecosystems organic matter cannot extract adequate quantities of energy from the organic matter and must be supplied with additional short chain carbon energy from living plants (Manske 2013a).

Renewable natural resource ecosystems that have improved soil quality and are functioning at or near potential capacity retain or recapture all of the essential elements used for biomass production during a growing season. About 4 to 5 times the quantity of essential elements contained in living organisms are held as immobilized organic compounds in the soil which prevents potential losses. Essential elements stored in the soil in the inorganic form are highly vulnerable to being lost through leaching, volatilization, and oxidation. A portion of the immobilized essential elements are mineralized by the soil microorganisms and made available to plants and other soil organisms that synthesize vital organic compounds of carbohydrates, proteins, and nucleic acids which are then used for additional growth (Manske 2012a).

The quantity of available essential elements in an ecosystem is dependent on the rate of mineralization of the soil organic matter by soil microorganisms. The larger the microorganism biomass, the greater the quantity of mineralized organic matter. Soil microorganisms are limited by access to simple carbohydrate energy. An increase in energy from short chain carbon compounds exudated from living plants, increases the biomass and activity of the soil microorganisms. Increased activity of soil microorganisms causes greater rates of mineralization that convert greater quantities of available inorganic essential elements resulting in greater quantities of ecosystem biomass production (Manske 2012a).

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Literature Cited

Bloem, J., D.W. Hopkins, and A. Benedetti (eds.). 2006. Microbiological methods for assessing soil quality. CAB International, Oxfordshire, UK. 307p.

Gibson, D.J. 2009. Grasses and grassland ecology. Oxford University Press Inc., New York, NY. 305p.

Manske, L.L. 2001. Mineral requirements for beef cows grazing native rangeland. NDSU Dickinson Research Extension Center. Range Management Report DREC 01-1033. Dickinson, ND. 13p.

Manske, L.L. 2008. Biologically efficient 12-month pasture and harvested forage management strategies for range cows. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 08-3050. Dickinson, ND. 3p.

Manske, L.L. 2012a. Degradation and biological restoration of mixed grass prairie ecosystems. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 12-3058. Dickinson, ND. 16p.

Manske, L.L. 2012b. Improvement of cropland soil quality through restoration of ecosystem biogeochemical processes. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 12-3059. Dickinson, ND. 4p.

Manske, L.L. 2013a. Perpetually sustainable grazingland ecosystems. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 13-3060. Dickinson, ND. 4p.

Manske, L.L., and S.A. Schneider. 2013b. Improvement of cropland soil quality through restoration of biogeochemical processes modeled after prototypical healthy biogeochemical processes of rangeland ecosystems. NDSU Dickinson Research Extension Center. Rangeland Research Outreach Program DREC 13-4020. Dickinson, ND. 66p.

Manske, L.L., and S.A. Schneider. 2013c. Proactive management of pestiferous rangeland grasshopper habitat of the Northern Plains. NDSU Dickinson Research Extension Center. Rangeland Research Outreach Program DREC 13-4021. Dickinson, ND.

Russelle, M.P. 1992. Nitrogen cycling in pastures and range. Journal of Production Agriculture 5:13-23.

Enhancement of the Nitrogen Cycle Improves Native Rangeland

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Available soil mineral nitrogen is the major limiting factor of herbage growth on native rangelands (Wight and Black 1979). Rangeland soils, however, are not deficient of nitrogen. Most of the nitrogen in rangeland ecosystems is in the organic form. A large amount of the organic nitrogen is immobilized in living tissue of microorganisms, plants, and animals as essential constituents of proteins and nucleic acids. An additional large amount of the soil organic nitrogen is contained in the soil organic matter detritus that is at various stages of physical breakdown and decomposition and is derived from dead organisms, excreta, and sloughed material. A small portion of the soil nitrogen is in the mineral form as ammonium, nitrate, and nitrite. The amount of available mineral nitrogen in the soil is affected by the rate of mineralization of the organic nitrogen by soil microorganisms. A minimum rate of mineralization of about 100 pounds of mineral nitrogen per acre per year is required to sustain herbage production at potential levels on native rangeland (Wight and Black 1972). Mineralization at these high rates can not be obtained from traditional grazing practices (Wight and Black 1972). Grazing management specifically designed to enhance soil microorganism activity can be implemented to obtain mineralization rates of 100 pounds of mineral nitrogen per acre per year or greater. Enhancement of the nitrogen cycle, with increases in the quantity of available soil mineral nitrogen, increases herbage growth and production and improves new wealth generation from native rangeland natural resources.

The nitrogen cycle in rangeland ecosystems is complex. Nitrogen is versatile and has several oxidation states and can exist as a gas, a dissolved cation or anion, a precipitated salt, an adsorbed or interlayer ion in clay, and as dissolved or solid organic molecules of varying complexity (Russelle 1992). Nitrogen moves through a variety of biological and chemical pathways and the movement within the cycle is difficult to predict and highly variable among different climatic zones because the nitrogen cycle pathways are directly or indirectly influenced by regional temperature and moisture regimes. Biological pathways are also influenced by metabolic rates of microorganisms, plants, and animals (Russelle 1992). The nitrogen cycle in rangelands is open and has inputs (gains) that transfer in from outside sources and has outputs (losses) that transfer out of the ecosystem.

Nitrogen inputs on rangelands arrive through atmospheric pathways as wet deposits in rain, snow, or hail and as dry deposits of gases or minute particles. Lightning discharges cause atmospheric nitrogen (N_2) and oxygen (O_2) to combine and produce nitrogen oxides, mainly nitric acid (NO) and dinitrogen oxide (N_2O), that are deposited on rangeland in precipitation. Inorganic nitrogen, as ammonium (NH_4) and nitrate (NO_3), and complex organic compounds removed by erosive forces from distant soil surfaces are deposited on rangelands in precipitation, wind, and sometimes overland water movement. The ambient amount of wet and dry nitrogen deposition in temperate regions from natural sources is around 5 to 6 pounds per acre per year (Brady 1974). Nitrogen deposits from other sources are primarily nitrogen oxides expelled in the exhaust emissions from cars, aircraft, and factories. The amount of nitrogen deposits from sources related to anthropogenic activity is highly variable, influenced by distance and direction from population centers, and can range from 0 to 15 pounds per acre per year or greater (Gibson 2009).

Symbiotic and nonsymbiotic fixation of atmospheric nitrogen is an input source of nitrogen for some mesic grasslands but generally not for semiarid rangelands. Strains of symbiotic Rhizobium bacteria form nodules on the roots of legumes and can fix atmospheric dinitrogen gas (N_2) in soil air and synthesize it into complex forms. Some of this fixed nitrogen is required by the bacteria, some of the nitrogen can be available to the host plant, and some of the nitrogen can be passed into the surrounding soil by excretion or by the sloughing off of the roots with nodules (Brady 1974). Legumes are not an abundant component in native rangelands and the legumes that are present in mature soils have low levels of nodulation and may not fix nitrogen (Gibson 2009). A few nonsymbiotic soil microorganisms are able to fix atmospheric dinitrogen (N_2) from soil air into their body tissue (Brady 1974). Nitrogen fixation by free living soil bacteria in semiarid rangelands is not known to be important and considered to be insignificantly low or nonexistent (Legg 1995, Gibson 2009).

Potential outputs for nitrogen from rangeland ecosystems can be lost to the atmosphere through denitrification of mineral nitrogen, ammonia volatilization, and volatilization by fire; lost through transfers by wind and water erosion of surface soil and by hydrologic leaching; and lost through animal production of both domesticated livestock and wildlife.

Denitrification is the reduction of inorganic nitrogen by removal of oxygen from the nitrite (NO_2) and nitrate (NO_3) mineral nitrogen to form gaseous nitrous oxides (NO and N_2O) or nonreactive dinitrogen gas (N_2) and can be mediated both chemically and biologically (Brady 1974). Losses from denitrification in rangelands is greatest in the nitrous oxide form (N_2O), followed by losses in the dinitrogen form (N_2). Losses in the nitric oxide form (NO) occur on rangelands only under acid conditions (Brady 1974). Chemical denitrification is of little importance in native rangelands unless nitrate is present in high concentrations (Russelle 1992). Biological denitrification occurs when soil microorganisms are deficient of oxygen as a result of poor drainage or poor soil structure causing soil saturation or lack of aeration. Denitrification probably accounts for only a small part of the total nitrogen losses from pastures and rangelands (Legg 1975, Gibson 2009).

Ammonia volatilization can occur near the soil surface during mineralization of soil organic nitrogen by soil microorganisms (Foth 1978). Gaseous ammonia (NH_3) forms as an intermediate stage and is usually readily hydrolyzed to form ammonium (NH_4) which is a stable form of mineral nitrogen. However, under conditions of increasing aridity and decreasing availability of hydrogen ions, the hydrolyzation process decreases and the amount of ammonia that escapes into the atmosphere by volatilization increases (Gibson 2009).

Nitrogen contained in aboveground herbage and litter is volatilized when rangelands are burned by prescribed fire and wild fire. Combustion causes nitrogen losses approaching 90%, primarily as ammonia (NH_3), dinitrogen oxide (N_2O), and other nitrogen oxides (Russelle 1992). Little belowground nitrogen is volatilized when the soil is moist during a burn, however, when the soil is dry, belowground temperatures can increase enough to denature protein, killing portions of the grass crowns and root material and volatilizing some belowground nitrogen.

Nitrogen in soil, litter, and organic detritus can be transferred from one area to another through movement by wind and water. The transferred nitrogen is a loss from one area and a gain at the deposition area. Nitrogen losses through erosion removal are variable and influenced by live plant density, litter cover, extent of branching fiberous root systems, and soil infiltration rates. The quantity of nitrogen lost through erosional movement can be decreased with enhancement of the nitrogen cycle and improvement in productivity of the rangeland ecosystem (Russelle 1992).

Soluble nitrate (NO_3) moves downward in the soil profile with soil water. In mesic grasslands, nitrogen can be lost as a result of water movement below the rooting depth (Russelle 1992). None of the mineral nitrogen in western rangelands is lost by hydrologic leaching through the soil profile (Power 1970) because very little water moves below the three foot soil depth and water loss by leaching is low or nonexistent in arid and semiarid rangelands under cover of perennial vegetation (Brady 1974, Wight and Black 1979).

Livestock grazing semiarid rangelands in the Northern Plains consume about 25% of the aboveground herbage, leaving a significant part of the nitrogen absorbed by the growing vegetation in the remaining live aboveground herbage, the standing dead vegetation, and the litter. Most of the nitrogen consumed by grazing livestock and wildlife is returned to the soil surface in urine and feces waste. Almost all of the nitrogen in urine is immediately available to plants. A portion of the urea in urine can be volatilized in warm dry conditions (Gibson 2009). Grazing animals retain only a small amount of the nitrogen consumed, about 15% to 17% in a nonlactating animal and about 30% in a lactating animal (Russelle 1992). The quantity of nitrogen lost as animal product increases as enhancement of the nitrogen cycle improves productivity of the rangeland ecosystem.

Differences in nitrogen inputs and outputs on rangeland soils determine the quantity of net accumulation of nitrogen. The total nitrogen content in soils accumulates gradually over several thousand years. Organic matter accumulation is benefitted in northern soils because little or no chemical oxidation activity of organic matter takes place during the cold periods. The dark surface layer of most soils in the Northern Plains has an accumulation of 2% to 5% organic matter (Larson et al. 1968, Wright et al. 1982). An acre of soil 6 inches deep contains about 1000 pounds of nitrogen for each percent of organic matter (Foth 1978). Nitrogen content and percent organic matter decrease with soil depth. A net accumulation of 2 pounds of nitrogen per acre per year results in a soil with 5 tons of nitrogen per acre in 5000 years.

The nitrogen cycle within rangeland soils functions around the two processes of immobilization and mineralization. These processes take place simultaneously with plant growth, dieback, and decomposition (Legg 1975). Immobilization is the process of tying up nitrogen in organic forms. Mineralization is the process of converting organic nitrogen into mineral (inorganic) nitrogen.

Biological immobilization of nitrogen occurs when autotrophic plants and soil microorganisms absorb inorganic nitrogen and build essential organic nitrogen compounds of amino acids and nucleic acids. Amino acids are building blocks of proteins that form enzymes, hormones, and important structural components of cells. Nucleic acids, deoxyribonucleic acid (DNA) and ribonucleic acid (RNA), are the genetic material that control all cellular functions and heredity. In rangeland soils, nitrogen is tied up in organic forms for three to four years (Power 1972). Biological immobilization of mineral nitrogen by plants and soil microorganisms is beneficial for rangeland ecosystems because about 95% of the total nitrogen is preserved within the soil as organic nitrogen and not subjected to great potential losses through denitrification and ammonia volatilization (Legg 1975, Gibson 2009).

Chemical immobilization of mineral nitrogen by adsorption of ammonium onto clay particles can be an advantage or a disadvantage for rangeland ecosystems depending on the type and amount of clay present. The ammonium ions are apparently the right size to fit into the cavities between crystal units normally occupied by potassium making the ammonium more or less a rigid part of the crystal (Brady 1974, Foth 1978). The type of clay mineral affects the retention of the ammonium. Clay materials with expanding lattices, such as vermiculite, illite, and montmorillonite, have greater surface area and adsorptive capacity for ammonium than clay minerals with nonexpanding lattices, such as kaolinite (Brady 1974, Legg 1975). Chemical immobilization of ammonium to clay material protects that portion of the soil mineral nitrogen from potential losses. The ammonium is slowly released from the clay and made available to plants and soil microorganisms. When the quantity of clay is too high or when the ammonium release rate is too slow, available mineral nitrogen may be too low to maintain ecosystem productivity at potential levels.

Mineralization occurs when organic nitrogen immobilized in living tissue or contained in soil organic matter detritus is processed by soil microorganisms to form mineral nitrogen. Mineralization consists of a series of reactions. Complex proteins and other organic nitrogen compounds are simplified by enzymatic digestion that hydrolyze the peptide bonds and liberate and degrade the amino acids by deamination to produce ammonia (NH_3) and carbon dioxide, or other low molecular weight carbon compounds (Power 1972, Brady 1974). Most of the released ammonia is readily hydrolyzed into ammonium (NH_4) which becomes part of the inorganic nitrogen pool in the soil.

Some of the ammonium produced during the mineralization process by soil microorganisms or the ammonium released from adsorption to clay material is nitrified in a complex two stage process coordinated by two distinct groups of soil bacteria. Ammonium is nitrified by enzyme oxidation that releases energy for the first group of bacteria and produces nitrite (NO_2) and water. In short order, the second group of bacteria oxidize the nitrite by enzyme activity that releases energy and produces nitrate (NO_3) which becomes part of the inorganic nitrogen pool in the soil. The speed of this coordinated two stage nitrification process prevents accumulation of nitrite in the soil. Concentrations of nitrite are toxic to higher plants (Brady 1974).

The quantity of available soil mineral nitrogen varies cyclically with changes in soil temperature, soil microorganism biomass, and plant phenological growth and development during the growing season (Whitman 1975) and is the net difference between the total quantity of organic nitrogen mineralized by soil microorganisms and the quantity of mineral nitrogen immobilized by plants (Brady 1974, Legg 1975). The relationships between soil microorganism activity and phenology of plant growth activity results in a dynamic cycle of available mineral nitrogen (Goetz 1975). When soil microorganism activity is greater than plant growth activity, the quantity of available mineral nitrogen increases. When plant growth activity is greater than soil microorganism activity, the quantity of available mineral nitrogen decreases. This cycle in available soil mineral nitrogen results in three peaks and three low periods during the growing season (Whitman 1975). The quantity of mineral nitrogen increases an average of 25% to 50% between the low periods and the peaks in the cycle with some variations occurring on different range sites and at different soil depths (Goetz 1975).

Mineralization and nitrification processes of soil microorganism activity start slowly in the spring when the soil temperature permits formation of liquid water around 30° F. Available mineral nitrogen increases with increases in soil temperature and microorganism biomass reaching the first peak in mineral nitrogen around mid May just prior to start of rapid plant growth. The quantity of mineral nitrogen decreases rapidly with increasing plant growth rates during spring reaching the first low period during June and the first two weeks of July. The second peak in mineral nitrogen is reached at the end of the active growing season usually around late July or early August. A second low period in mineral nitrogen occurs from around mid August to mid or late September when plants have slow growth rates and during growth and development of fall tillers and fall tiller buds that will produce the early plant growth during the subsequent growing season. The third peak in mineral nitrogen occurs around mid October just prior to the end of the perennial plant growing season during autumn. Mineral nitrogen declines during the third low period as winter freeze up approaches (Goetz 1975, Whitman 1975).

The greater the quantity of mineral nitrogen available during periods of active plant growth, the greater the quantity of herbage biomass production. Rangeland ecosystem biogeochemical processes that cycle nitrogen need to function at rates that provide 100 pounds of mineral nitrogen per acre to produce the minimum potential quantity of herbage biomass and need to provide 165 pounds of mineral nitrogen per acre to produce the maximum potential quantity of herbage biomass (Wight and Black 1972) (table 1).

Traditional management practices, like 6.0 month seasonlong, repeated seasonal, and deferred grazing, were designed to use rangelands as a source of grazable forage for livestock and, even when operated with strong land stewardship ethics, traditional practices do not provide mineral nitrogen at quantities great enough to produce the potential quantity of herbage. Rangelands managed for about 35 years with a moderately stocked 6.0 month seasonlong grazing practice provided 62 pounds of mineral nitrogen per acre (Manske 2009), rangelands managed with an unspecified traditional grazing practice provided 59 pounds of mineral nitrogen per acre (Wight and Black 1972), and rangelands managed for 35 years with a low to moderately stocked 4.5 to 5.0 month deferred grazing practice provided 31 pounds of mineral nitrogen per acre (Manske 2008) (table 1). Rangelands managed with traditional grazing practices provide mineral nitrogen at deficiency rates of less than 100 pounds per acre causing decreases in plant water use efficiency and reducing herbage biomass production an average of 49.6% per inch of precipitation (Wight and Black 1979) (table 1). As a consequence of traditional grazing practices providing low quantities of mineral nitrogen and producing less than potential quantities of herbage biomass, native rangelands are incorrectly considered to be low producing, low income generating, resources.

Grazing management that is designed to meet the biological requirements of the plants and soil microorganisms and to stimulate ecosystem biogeochemical processes provide greater quantities of mineral nitrogen than do traditional practices. During the seventh grazing season, rangelands managed with a three pasture twice-over rotation grazing system provided 178 pounds of mineral nitrogen per acre (Manske 2008) (table 1). The greater quantity of mineral nitrogen resulted from greater soil microorganism activity. The twice-over rotation grazing system stimulated soil microorganism activity in the rhizosphere by increasing the quantity of plant fixed carbon exudated through grass roots into the rhizosphere. Removal of 25% to 33% of the leaf material by grazing livestock after the three and a half new leaf stage and before the flowering (anthesis) stage increased plant carbon exudates (Manske 2007). Soil microorganism growth and activity is limited by available carbon. Rhizosphere organisms increase in biomass and activity with increases in carbon. The rhizosphere volume on traditional grazing practices after twenty years of 6.0 month seasonlong and 4.5 month seasonlong was 50 and 68 cubic feet per acre, respectively (table 1). The rhizosphere volume was 227 cubic feet per acre on a twice-over rotation grazing system after twenty years (Manske 2008) (table 1). The greater rhizosphere organism biomass on rangelands managed with a twice-over rotation system had increased activity that mineralized and nitrified a greater quantity of organic nitrogen into mineral nitrogen. The greater quantity of available soil mineral nitrogen permitted the production of maximum potential herbage biomass, the growth of greater pounds of calf weight per acre, the generation of greater wealth per acre, and the improvement of native rangeland natural resources (Manske et al. 2008).

Table 1. Grazing management effects on mineral nitrogen and rhizosphere volume in native rangelands.

Standards for Mineral Nitrogen		Mineral Nitrogen	Source
Minimum potential herbage biomass		100 lbs/ac	Wight and Black 1972
Maximum potential herbage biomass		165 lbs/ac	Wight and Black 1972
Mineral nitrogen deficiency of less than 100 lbs/ac results in 49.6% reduction in herbage production per inch of precipitation.			Wight and Black 1979
Grazing Management		**Mineral Nitrogen**	
4.5-5.0 month Deferred	35 yrs	31 lbs/ac	Manske 2008
Traditional, not specified	long-term	59 lbs/ac	Wight and Black 1972
6.0 month Seasonlong	35 yrs	62 lbs/ac	Manske 2009
4.5 month Seasonlong	6 yrs	77 lbs/ac	Manske 2008
Twice-over Rotation	6 yrs	178 lbs/ac	Manske 2008
Grazing Management		**Rhizosphere Volume**	
6.0 month Seasonlong	20 yrs	50 ft^3/ac	Manske 2008
4.5 month Seasonlong	20 yrs	68 ft^3/ac	Manske 2008
Twice-over Rotation	20 yrs	227 ft^3/ac	Manske 2008

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Literature Cited

Brady, N.C. 1974. The nature and properties of soils. MacMillan Publishing Co. Inc., New York, NY. 639p.

Foth, H.D. 1978. Fundamentals of soil science. John Wiley and Sons, New York, NY. 436p.

Gibson, D.J. 2009. Grasses and grassland ecology. Oxford University Press Inc., New York, NY. 305p**.**

Goetz, H. 1975. Availability of nitrogen and other nutrients on four fertilized range sites during the active growing season. Journal of Range Management 28:305-310.

Larson, K.E., A.F. Bahr, W. Freymiller, R. Kukowski, D. Opdahl, H. Stoner, P.K. Weiser, D. Patterson, and O. Olsen. 1968. Soil survey of Stark County, North Dakota. U.S. Government Printing Office, Washington, D.C. 116p.+plates.

Legg, J.O. 1975. Influence of plants on nitrogen transformation in soils. pg. 221-227. *in* M.K. Wali (ed.). Prairie: A multiple view. University of North Dakota Press. Grand Forks, ND.

Manske, L.L. 2007. Biology of defoliation by grazing. NDSU Dickinson Research Extension Center. Range Management Report DREC 07-1067. Dickinson, ND. 25p.

Manske, L.L. 2008. Grazing and burning treatment effects on soil mineral nitrogen and rhizosphere volume. NDSU Dickinson Research Extension Center. Range Research Report DREC 08-1066b. Dickinson, ND. 15p.

Manske, L.L., and S.A. Schneider. 2008. Biologically effective management of grazinglands. 2nd Edition. NDSU Dickinson Research Extension Center. Rangeland Research Extension Program 4012. Dickinson, ND. 181p.

Manske, L.L. 2009. Nitrogen fertilization of native rangeland with ammonium nitrate and urea. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1069. Dickinson, ND. 38p.

Power, J.F. 1970. Nitrogen management of semiarid grasslands in North America. Proceedings of the XI International Grassland Congress. 1970:468-471.

Power, J.F. 1972. Fate of fertilizer nitrogen applied to a Northern Great Plains rangeland ecosystem. Journal of Range Management 25:367-371.

Russelle, M.P. 1992. Nitrogen cycling in pastures and range. Journal of Production Agriculture 5:13-23.

Whitman, W.C. 1975. Native range fertilization and interseeding study. Annual Report. Dickinson Experiment Station. Dickinson, ND. p. 11-16.

Wight, J.R., and A.L. Black. 1972. Energy fixation and precipitation use efficiency in a fertilized rangeland ecosystem of the Northern Great Plains. Journal of Range Management 25:376-380.

Wight, J.R., and A.L. Black. 1979. Range fertilization: plant response and water use. Journal of Range Management 32:345-349.

Wright, M.R., J. Schaar, and S.J. Tillotson. 1982. Soil survey of Dunn County, North Dakota. U.S. Government Printing Office, Washington, D.C. 235p.+plates.

Soil Mineral Nitrogen Increased Above the Threshold Quantity of 100 Pounds per Acre in Rangeland Ecosystems

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Rangelands are valuable assets to livestock agriculture in the Northern Plains and should be managed as renewable natural resources that generate economic wealth rather than be managed as places that produce forage for livestock. The major factors that regulate the amount of new wealth generated from rangelands are the quantity of mineral nitrogen available in the soil, and whether the grazing management strategy implemented is beneficial or antagonistic to the ecosystem biogeochemical processes that convert organic nitrogen into mineral nitrogen. Biologically effective grazing management strategies have been developed that beneficially meet the biological requirements of the grass plants and the rhizosphere organisms, and that enhance the microorganism biomass and activity levels sufficiently to convert organic nitrogen into mineral nitrogen at rates greater than 100 pounds per acre.

Native rangeland ecosystems in the Northern Plains that have less than 100 pounds of soil mineral nitrogen per acre do not produce herbage biomass at the biological potential quantities. Rehabilitation of this condition requires minimization of the inhibitory effects on the biogeochemical processes in the rangeland ecosystems caused by deficiencies in necessary elements, principally mineral nitrogen.

Growth of herbage biomass by rangeland grasses requires the essential major elements of carbon, hydrogen, and nitrogen in the presence of sunlight (Manske 2007, 2009d). Radiant energy from the sun is not limiting on rangelands even with about 30% cloud cover, except under the shade of taller shrubs. The source of carbon for plant growth is atmospheric carbon dioxide (CO_2) which composes about 0.03% of the gasses in the atmosphere, exists at concentrations of around 370 ppm, and is not limiting on rangelands. The hydrogen comes from soil water (H_20) absorbed through the roots and distributed throughout the plant within the xylem vascular tissue. Water has been deficient on western North Dakota rangelands at a long-term frequency of 32.7% of the 6.0 month perennial plant growing season from mid April to mid October during the 118 year period, 1892 to 2009 (Manske et al. 2010). Water is a necessary requirement for plant growth and has a dominant role in physiological processes, however, water does not limit herbage production on rangeland ecosystems to the extent that mineral nitrogen availability does (Wight and Black 1972). Deficiencies in mineral nitrogen limit herbage production more often than water in temperate grasslands (Tilman 1990). The source of nitrogen for plant growth on rangelands is mineral nitrogen (NO_3, NH_4) converted from soil organic nitrogen by rhizosphere organisms. The rate of mineralization of soil organic nitrogen into mineral nitrogen is dependant on the rhizosphere volume and microorganism biomass (Gorder, Manske, and Stroh 2004). The quantity of soil mineral nitrogen available at any point during the growing season is the net difference between the variable effects from the two opposing processes of immobilization and mineralization of soil nitrogen (Whitman 1975, Goetz 1975, Manske 2009e). These processes take place simultaneously with plant growth, dieback, and decomposition. Immobilization occurs when autotrophic plants and soil microorganisms absorb mineral nitrogen and build organic nitrogen compounds. Mineralization occurs when complex immobilized organic nitrogen compounds are simplified by processes of the rhizosphere microorganisms to form mineral nitrogen. Available soil mineral nitrogen is the major limiting factor of herbage growth on native rangeland ecosystems (Wight and Black 1979). A minimum rate of mineralization that supplies 100 pounds of mineral nitrogen per acre is required to sustain herbage production at biological potential levels on rangelands (Wight and Black 1972).

Soil mineral nitrogen available at the threshold quantity of 100 lbs/ac is required for activation of three ecological biogeochemical processes important for rangeland grass production. Wight and Black (1972, 1979) determined that the processes associated with precipitation (water) use efficiency in grass plants were not fully activated unless 100 lbs/ac of mineral nitrogen was available. Manske (2010a, 2010b) found evidence that two defoliation resistance mechanisms (Manske 1999, 2007) had threshold requirements for activation at 100 lbs/ac of mineral nitrogen.

Wight and Black (1972) found that precipitation use efficiency of rangeland grasses improved when soil mineral nitrogen was available at quantities greater than 100 lbs/ac. The inhibitory deficiencies of mineral nitrogen on rangelands 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 rangeland ecosystems that had greater than 100 lbs/ac of mineral nitrogen and did not have mineral nitrogen deficiencies (Wight and Black 1979). The quantity of herbage biomass production on rangeland ecosystems that have greater than 100 lbs/ac soil mineral nitrogen will be about double the quantity of herbage biomass production on rangeland ecosystems that have less than 100 lbs/ac soil mineral nitrogen, even during periods of water deficiency.

Manske (2010a, 2010b) found that partial defoliation of grass tillers at phenological growth stages between the three and a half new leaf stage and the flower (anthesis) stage activated the compensatory physiological processes (McNaughton 1979, 1983; Briske 1991) within grass plants that enabled partially defoliated grass tillers to rapidly and completely replace the leaf material removed by grazing, and activated the asexual processes of vegetative reproduction (Mueller and Richards 1986, Richards et al. 1988, Murphy and Briske 1992, Briske and Richards 1994, 1995) that produced secondary tillers from axillary buds in rangeland ecosystems that had soil mineral nitrogen available at quantities greater than 100 lbs/ac, however, the same defoliation treatments did not activate the defoliation resistance mechanisms of grass plants in rangeland ecosystems that had soil mineral nitrogen available at quantities less than 100 lbs/ac. Inhibitory mineral nitrogen deficiencies exist in rangeland ecosystems that have soil mineral nitrogen available at less than 100 lbs/ac and mineral nitrogen deficiencies do not occur in rangeland ecosystems that have soil mineral nitrogen available at 100 lbs/ac or greater (Wight and Black 1972, 1979; Manske 2010a, 2010b).

Full activation of the biogeochemical processes that improve water use efficiency in grass plants, that enable grass tillers to replace leaf material at greater amounts than removed by grazing, and that vegetatively reproduce secondary tillers occurs at biological potential rates only on rangeland ecosystems that have 100 lbs/ac or greater of soil mineral nitrogen available. As a result of full activation of these three processes, grass plants on rangeland ecosystems that have mineral nitrogen at 100 lbs/ac or greater are able to produce greater quantities of herbage per inch of precipitation received, recover rapidly from the effects of grazing and completely replace lost leaf material, produce greater vegetative tiller densities, and produce greater cow and calf weight on less land area than grass plants on rangeland ecosystems that have less than 100 lbs/ac soil mineral nitrogen available.

Since the early portions of the 20th century, the low herbage biomass production observed on native rangelands managed with traditional grazing practices has generally been accepted to be caused by the low levels of available soil mineral nitrogen in the ecosystem (Goetz 1984). The development of management practices that raise the quantity of soil mineral nitrogen in native rangeland ecosystems has been considered to be hugely important for increasing herbage biomass quantity and quality. Major research projects that related to some aspect of increasing soil mineral nitrogen in rangeland ecosystems have been conducted at the Dickinson Research Extension Center from 1956 through 2010. Numerous scientific endeavors to elevate the levels of soil mineral nitrogen on rangelands with the agronomical practices of nitrogen fertilization (Manske 2009e) and of interseeding alfalfa (Manske 2005) were conducted and extensively researched on the Northern Plains between 1951 and 2004 (Manske 2005, 2009e).

Application of nitrogen fertilizer to native rangeland did not solve the problems related to low soil mineral nitrogen. Nitrogen fertilization on degraded rangeland resulted in a small increase in production of herbage biomass per pound of fertilizer nitrogen, and in a short-term shift in plant species composition with an increase in mid cool season grasses and a decrease in short warm season grasses (Manske 2009e). Initially, these desired changes were considered to be beneficial (Manske 2009d). However, reevaluations of the data showed that the costs of the additional herbage weight were excessive (Manske 2009b), and that the long-term disruptions of ecosystem biogeochemical processes were detrimental to the native plant community (Manske 2010c). With the reduction of short warm season grasses, live plant basal cover decreased, exposing greater amounts of soil to higher levels of solar radiation and erosion (Goetz et al. 1978). These large areas of open spaces became ideal invasion sites for undesirable plants resulting in the long-term plant species composition shift to a replacement community of domesticated and introduced mid cool season grasses and in the removal of nearly all of the native plant species (Manske 2009a, 2010c).

Interseeding alfalfa into native rangeland did not solve the problems related to low soil mineral nitrogen. The demand on the existing low levels of soil mineral nitrogen in rangeland ecosystems increased with the introduction of alfalfa because almost all of the alfalfa plant nitrogen needs had to be taken from the soil. The interseeded alfalfa plants had extremely low levels of nodulation of rhizobium bacteria on the roots and, consequently, almost no nitrogen fixation (Manske 2004b). As a result of the low amounts of available mineral nitrogen, the interseeded alfalfa plants had slower rates of growth and higher rates of mortality then alfalfa plants solid seeded into cropland (Manske 2005). Furthermore, the alfalfa plants interseeded into rangeland depleted the soil water levels within a 5 foot radius of each crown an average of 35% below ambient soil water levels causing water stress conditions in the surrounding grass plants and, subsequently, reducing grass herbage biomass production (Manske 2004a, 2005).

Management of rangelands with agronomic principles did not effectively improve ecosystem nitrogen cycling processes and did not solve the problems related to low soil mineral nitrogen. However, the accumulation of scientific information gained from these extensive projects has provided insightful understanding into the complexity of the nitrogen cycle and plant growth in native rangeland ecosystems and contributed a substantial foundation of knowledge from which further progress developed. Identification of the defoliation resistance mechanisms and the biogeochemical processes associated with perennial grass plants and rhizosphere organisms on grassland ecosystems was the next set of essential scientific information needed. The missing factor in achieving healthy productive grasslands at that point was the development of an effective management strategy that could activate these beneficial mechanisms. The emphasis of later research projects was transferred to management of rangelands with ecological principles that progressed into the successful development of a biologically effective grazing strategy that increased soil mineral nitrogen above the threshold quantity of 100 pounds per acre (Manske 1999, 2007, 2008).

Rangeland soils are not deficient of nitrogen. Most of the nitrogen has been immobilized in the soil as organic nitrogen (Legg 1975). The organic nitrogen must be converted into mineral nitrogen in order for soil nitrogen to be available to rangeland plants. The quantity of available mineral nitrogen in rangeland ecosystem soils is dependant on the rate of mineralization of soil organic nitrogen by rhizosphere organisms. The larger the rhizosphere volume and microorganism biomass, the greater the quantity of soil mineral nitrogen converted (Coleman et al. 1983, Ingham et al. 1985). Rhizosphere volume and microorganism biomass are limited by access to carbon and energy from simple carbohydrates because the primary microflora trophic levels (bacteria and endomycorrhizal fungi) in the rhizosphere lack chlorophyll and have low carbon (energy) content (Anderson et al. 1981, Curl and Truelove 1986, Whipps 1990). Healthy grass plants capture and fix carbon during photosynthesis and produce carbohydrates in quantities greater than the amount needed for tiller growth and development (Coyne et al. 1995). Partial defoliation of grass tillers that removes about 25% to 33% of the aboveground leaf material at vegetative phenological growth stages between the three and a half new leaf stage and the flower (anthesis) stage (Manske 2007, 2009c) by large grazing herbivores causes greater quantities of exudated material containing simple carbohydrates to be released from the grass tillers through the roots into the rhizosphere (Hamilton and Frank 2001). With the increase in availability of carbon compounds in the rhizosphere, the biomass and activity of the microorganisms increases (Anderson et al. 1981, Curl and Truelove 1986, Whipps 1990). The increase in rhizosphere organism biomass and activity causes greater rates of mineralization of soil organic nitrogen and results in greater quantities of available mineral nitrogen (Coleman et al. 1983, Clarholm 1985, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005). The twice-over rotation grazing management system is the biologically effective management strategy that is coordinated with grass phenological growth stages and meets the biological requirements of the perennial grass plants and rhizosphere organisms and that increases rhizosphere activity to mineralize nitrogen at quantities greater than 100 lbs/ac (Manske 1999, 2007, 2010b)

Rangeland ecosystems managed with traditional grazing practices have inhibitory mineral nitrogen deficiencies. Traditional seasonlong grazing practices have soil mineral nitrogen available at low quantities ranging between 59 lbs/ac during mid July (Wight and Black 1972) and 77 lbs/ac during late June (Manske 2010b), and the popular deferred grazing practice has soil mineral nitrogen available at the very low quantity of 31 lbs/ac during mid July (Manske 2008) (table 1).

The rhizosphere organisms on rangeland ecosystems that have less than 100 lbs/ac soil mineral nitrogen available amass in number for about three growing seasons after the biologically effective partial defoliation grazing methods are initiated before the microorganism biomass and activity levels are enhanced sufficiently to be able to mineralize soil organic nitrogen at rates that supply greater than 100 pounds of soil mineral nitrogen per acre. Mineralization rates that have been reached through the biologically effective stimulation grazing methods have ranged between 164 lbs/ac and 199 lbs/ac soil mineral nitrogen available in the top 1 foot of soil during late June (Manske 2008) (table 1). Rhizosphere organisms require elevated quantities of simple carbohydrates exudated from the roots of perennial grass plants annually defoliated by large grazing herbivores removing about 25% to 33% of the aboveground leaf material during the vegetative phenological growth stages between the three and a half new leaf stage and the flower stage to maintain mineralization rates at greater than 100 lbs/ac soil mineral nitrogen.

The threshold quantity of soil mineral nitrogen at 100 lbs/ac or greater during mid to late June is required to fully activate three significant biogeochemical processes; the water use efficiency processes, the compensatory physiological processes, and the asexual vegetative reproduction processes in rangeland grass plants. These important findings give rangeland managers the first quantitative standard from which the condition of an ecosystem can be judged as healthy or unhealthy. In the near future, the health and ecological status of any rangeland ecosystem will be quantitatively evaluated by a simple measurement of available soil mineral nitrogen. Rangeland ecosystems that have soil mineral nitrogen available at quantities greater than 100 lbs/ac are functioning above biological potential production capacity and rangeland ecosystems that have soil mineral nitrogen available at quantities less than 100 lbs/ac have a soil mineral nitrogen deficiency and are functioning below biological potential production capacity.

The quantities of soil mineral nitrogen available at other time periods during the entire perennial grass growing season, mid April to mid October, need to be determined for grazed rangeland ecosystems in the Northern Plains. It is unlikely that the quantity of soil mineral nitrogen is a stationary value through the growing season. Soil mineral nitrogen in native rangeland ecosystems is most likely available in dynamic cycles with peaks and valleys during the growing season (Goetz 1975). The threshold quantity of 100 lbs/ac most likely represents the minimum amount of soil mineral nitrogen available in a healthy fully functioning rangeland ecosystem at any time during the growing season.

Rangelands in the Northern Plains have been perceived to have low productivity levels because the economic returns from livestock agriculture have usually been low. Low returns from rangelands have not been caused by inherent negative characteristics of rangeland ecosystems but have been caused by management induced problems. Low productivity on rangelands has resulted from the low quantity of available mineral nitrogen that was caused by the antagonistic effects from traditional grazing management practices on the rhizosphere organisms and the biogeochemical processes reducing the amount of organic nitrogen converted into mineral nitrogen. Beneficial biologically effective grazing management strategies stimulate rhizosphere organism activities and ecosystem biogeochemical processes that increase the quantity of available soil mineral nitrogen to exceed 100 pounds per acre. Soil mineral nitrogen available at 100 lbs/ac or greater results in increased herbage and forage nutrient production, improved cow and calf performance, improved efficiency of forage nutrient capture, and improved efficiency of the conversion of forage nutrients into saleable commodities of livestock weight which are essential for the beef production industry to achieve actual reductions in forage feed costs and increases in the quantity of new wealth generated from rangelands.

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Table 1. Soil mineral nitrogen quantity and rhizosphere volume.

Grazing Management Practice	Mineral Nitrogen lbs/ac-ft	Rhizosphere Volume ft^3/ac-ft
4.5-5.0 month Deferred	31	-
Traditional Seasonlong	59	-
6.0 month Seasonlong	62	50
4.5 month Seasonlong	77	68
Twice-over Rotation	178	227
1st pasture grazed	199	-
2nd pasture grazed	164	-
3rd pasture grazed	171	-

Literature Cited

Anderson, R.V., D.C. Coleman, C.V. Cole, and E.T. Elliott. 1981. Effect of nematodes *Acrobeloides sp.* and *Mesodiplogaster lheritieri* on substrate utilization and nitrogen and phosphorus mineralization. Ecology 62:549-555.

Bird, S.B., J.E. Herrick, M.M. Wander, and S.F. Wright. 2002. Spatial heterogeneity of aggregate stability and soil carbon in semi-arid rangeland. Environmental Pollution 116:445-455.

Briske, D.D. 1991. Developmental morphology and physiology of grasses. p. 85-108. *in* R.K. Heitschmidt and J.W. Stuth (eds.). Grazing management: an ecological perspective. Timber Press, Portland, OR.

Briske, D.D., and J.H. Richards. 1994. Physiological responses of individual plants to grazing: current status and ecological significance. p. 147-176. *in* M. Vavra, W.A. Laycock, and R.D. Pieper (eds.). Ecological implications of livestock herbivory in the west. Society for Range Management, Denver, CO.

Briske, D.D., and J.H. Richards. 1995. Plant response to defoliation: a physiological, morphological, and demographic evaluation. p. 635-710. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Burrows, R.L., and F.L. Pfleger. 2002. Arbuscular mycorrhizal fungi respond to increasing plant diversity. Canadian Journal of Botany 80:120-130.

Clarholm, M. 1985. Interactions of bacteria, protozoa, and plants leading to mineralization of soil nitrogen. Soil Biology and Biochemistry 17:181-187.

Coleman, D.C., C.P.P. Reid, and C.V. Cole. 1983. Biological strategies of nutrient cycling in soil ecosystems. Advances in Ecological Research 13:1-55.

Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995. Carbon and nitrogen dynamics in range plants. p. 59-167. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and development morphology. Society for Range Management, Denver, CO.

Curl, E.A., and B. Truelove. 1986. The rhizosphere. Springer-Verlag, New York, NY.

Driver, J.D., W.E. Holben, and M.C. Rillig. 2005. Characterization of glomalin as a hyphal wall component of arbuscular mycorrhizal fungi. Soil Biology and Biochemistry 37:101-106.

Goetz, H. 1975. Availability of nitrogen and other nutrients on four fertilized range sites during the active growing season. Journal of Range Management 28:305-310.

Goetz, H. 1984. A synopsis of rangeland fertilization in western North Dakota. p. 17-27. *in* Proceedings of North Dakota Chapter of the Society for Range Management, 1983. Dickinson, ND.

Goetz, H., P.E. Nyren, and D.E. Williams. 1978. Implications of fertilizers in plant community dynamics of Northern Great Plains rangelands. Proceedings of the First International Rangeland Congress. p. 671-674.

Gorder, M.M., L.L. Manske, and T.L. Stroh. 2004. Grazing treatment effects on vegetative tillering and soil rhizospheres of western wheatgrass. NDSU Dickinson Research Extension Center. Range Research Report DREC 04-1056. Dickinson, ND. 13p.

Hamilton, E.W., and D.A. Frank. 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82:2397-2402.

Ingham, R.E., J.A. Trofymow, E.R. Ingham, and D.C. Coleman. 1985. Interactions of bacteria, fungi, and the nemotode grazers: effects of nutrient cycling and plant growth. Ecological Monographs 55:119-140.

Klein, D.A., B.A. Frederick, M. Biondini, and M.J. Trlica. 1988. Rhizosphere microorganism effects on soluble amino acids, sugars, and organic acids in the root zone of *Agropyron cristatum*, *A. smithii*, and *Bouteloua gracilis*. Plant and Soil 110:19-25.

Legg, J.O. 1975. Influence of plants on nitrogen transformation in soils. pg. 221-227. *in* M.K. Wali (ed.). Prairie: A multiple view. University of North Dakota Press. Grand Forks, ND.

Manske, L.L. 1999. Can native prairie be sustained under livestock grazing? p. 99-108. *in* J. Thorpe, T.A. Steeves, and M. Gollop (eds.). Provincial Museum of Alberta. Natural History Occasional Paper No. 24. Edmonton, Alberta.

Manske, L.L. 2004a. Evaluation of interseeding row-spacing techniques. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 04-3033. Dickinson, ND. 16p.

Manske, L.L. 2004b. Evaluation of interseeding seeding-date, seeding-rate, and rhizobium-inoculation techniques. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 04-3036. Dickinson, ND. 13p.

Manske, L.L. 2005. Evaluation of alfalfa interseeding techniques. NDSU Dickinson Research Extension Center. Rangeland Research Extension Program 4008. 140p.

Manske, L.L. 2007. Biology of defoliation by grazing. NDSU Dickinson Research Extension Center. Range Management Report DREC 07-1067. Dickinson, ND. 25p.

Manske, L.L. 2008. Grazing and burning treatment effects on soil mineral nitrogen and rhizosphere volume. NDSU Dickinson Research Extension Center. Range Research Report DREC 08-1066b. Dickinson, ND. 15p.

Manske, L.L. 2009a. Evaluation of plant species shift on fertilized native rangeland. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1071. Dickinson, ND. 23p.

Manske, L.L. 2009b. Cost of herbage weight for nitrogen fertilization treatments on native rangeland. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1072. Dickinson, ND. 10p.

Manske, L.L. 2009c. Grass plant responses to defoliation. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1074. Dickinson, ND. 47p.

Manske, L.L. 2009d. Influence of soil mineral nitrogen on native rangeland plant water use efficiency and herbage production. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 09-3053. Dickinson, ND. 3p.

Manske, L.L. 2009e. Evaluation of nitrogen fertilization on native rangeland. NDSU Dickinson Research Extension Center. Rangeland Research Outreach Program 4013. 168p.

Manske, L.L. 2010a. Leaf stage development of western wheatgrass tillers. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1075. Dickinson, ND. 48p.

Manske, L.L. 2010b. Evaluation of the defoliation resistance mechanisms influence on vegetative tiller initiation and tiller density. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1076. Dickinson, ND. 13p.

Manske, L.L. 2010c. Long-term plant species shift caused by nitrogen fertilization of native rangeland. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 10-3055. Dickinson, ND. 16p.

Manske, L.L., S. Schneider, J.A. Urban, and J.J. Kubik. 2010. Plant water stress frequency and periodicity in western North Dakota. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1077. Dickinson, ND. 11p.

McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist 113:691-703.

McNaughton, S.J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329-336.

Mueller, R.J., and J.H. Richards. 1986. Morphological analysis of tillering in *Agropyron spicatum* and *Agropyron desertorum.* Annals of Botany 58:911-921.

Murphy, J.S., and D.D. Briske. 1992. Regulation of tillering by apical dominance: chronology, interpretive value, and current perspectives. Journal of Range Management 45:419-429.

Richards, J.H., R.J. Mueller, and J.J. Mott. 1988. Tillering in tussock grasses in relation to defoliation and apical bud removal. Annals of Botany 62:173-179.

Rillig, M.C., S.F. Wright, and V.T. Eviner. 2002. The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. Plant and Soil 238:325-333.

Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58:3-15.

Whipps, J.M. 1990. Carbon economy. p. 59-97. *in* J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

Whitman, W.C. 1975. Native range fertilization and interseeding study. Annual Report. Dickinson Experiment Station. Dickinson, ND. p. 11-16.

Wight, J.R., and A.L. Black. 1972. Energy fixation and precipitation use efficiency in a fertilized rangeland ecosystem of the Northern Great Plains. Journal of Range Management 25:376-380.

Wight, J.R., and A.L. Black. 1979. Range fertilization: plant response and water use. Journal of Range Management 32:345-349.

Influence of Soil Mineral Nitrogen on Native Rangeland Plant Water Use Efficiency and Herbage Production

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Report DREC 09-3053

Native rangelands managed by traditional grazing practices are deficient in available soil mineral nitrogen and produce less than potential quantities of herbage biomass (Wight and Black 1972). The biogeochemical processes of these rangeland ecosystems typically function at levels that cycle nitrogen at rates of about 59 pounds or less of mineral nitrogen per acre per year and produce only one half to one third of the potential quantities of herbage biomass (Wight and Black 1972). The remedy for the problem of low herbage production on native rangeland is not repetitive applications of nitrogen fertilizer because the additional herbage produced from nitrogen fertilization has unprofitably high costs (Manske 2009b) and the long-term effects from nitrogen fertilization cause shifts in plant species composition with reductions of the native grass species and increases of the domesticated and introduced grass species (Manske 2009a). However, the results from more than three decades of nitrogen fertilization research on native rangelands provides insight into the underlying causes of the problem of herbage production at below potential quantities on native rangelands managed by traditional grazing practices.

Nitrogen fertilization of native rangeland increases the quantity of available soil mineral nitrogen. Total herbage biomass production on native rangeland increases with the increases in quantity of soil mineral nitrogen (Rogler and Lorenz 1957, Whitman 1957, Whitman 1963, Smika et al. 1965, Goetz 1969, Power and Alessi 1971, Lorenz and Rogler 1972, Goetz 1975, Taylor 1976, Whitman 1976, Goetz et al. 1978, Wight and Black 1979). The greater quantities of available soil mineral nitrogen cause the soil water use efficiency to improve in grassland plants (Smika et al. 1965, Wight and Black 1972, Whitman 1976, 1978). Water use efficiency (pounds of herbage produced per inch of water use) is difficult to measure quantitatively because soil water can be lost through evaporation or transpiration. Precipitation use efficiency (pounds of herbage produced per inch of precipitation received) is less complicated to measure than water use efficiency. Wight and Black (1972) found that precipitation use efficiency of grasslands improved with increased quantities of soil mineral nitrogen and that the pounds of herbage produced per inch of precipitation were greater on the nitrogen fertilized treatments than on the unfertilized treatments. Wight and Black (1979) compared herbage production on traditionally managed rangeland with the typical ambient deficiency of available mineral nitrogen to herbage production on nitrogen fertilized rangeland without a deficiency of available mineral nitrogen. During ten years of study with normal growing season precipitation, the deficiency of mineral nitrogen on the traditionally managed rangeland caused the weight of herbage production per inch of precipitation received to be reduced an average of 49.6% below the herbage produced per inch of precipitation on the rangeland without a mineral nitrogen deficiency.

Nitrogen cycling in Northern Plains rangeland ecosystems managed by traditional grazing practices is inadequate to supply the quantity of mineral nitrogen necessary for minimum potential herbage production. A deficiency in available mineral nitrogen causes reductions in grassland plant water use efficiency and reductions in herbage biomass production to below potential levels during growing seasons with normal precipitation and no deficiency in available water. During growing seasons with below normal precipitation, both the deficiency in available water and the deficiency in available mineral nitrogen contribute to the resulting reductions in herbage production. During drought growing seasons, the percent reduction in herbage production is greater than the percent reduction in precipitation because of the additional reductions in water use efficiency and herbage production caused by the deficiency of mineral nitrogen. Semiarid rangelands would produce herbage biomass at the maximum level for whatever soil water was available if the ecosystems were not deficient in mineral nitrogen (Power and Alessi 1971). Herbage production on native rangeland ecosystems at minimum potential herbage yields would require nitrogen cycling at a rate of about 100 pounds of available mineral nitrogen per acre per year and that maximum potential herbage yields would be produced at rates of about 165 pounds of mineral nitrogen per acre per year (Wight and Black 1972).

Native rangeland plants need hydrogen, carbon, and nitrogen to produce herbage biomass. The hydrogen comes from soil water absorbed through the roots. The carbon comes from atmospheric carbon dioxide fixed through photosynthesis in the leaves. The nitrogen comes from the mineral nitrogen mineralized from soil organic nitrogen by rhizosphere microorganisms (Manske 2007). The total amount of energy fixed by chlorophyllous plants on rangeland ecosystems is not limited by the availability of radiant energy from the sun or by the availability of atmospheric carbon dioxide. The availability of water, which is an essential requirement for plant growth and has a dominant role in physiological processes, does not limit herbage production on rangeland ecosystems to the extent that mineral nitrogen availability does (Wight and Black 1972). Available soil mineral nitrogen is the major herbage growth limiting factor in Northern Plains rangelands (Wight and Black 1979). Grassland soils are not deficient of nitrogen and do not require application of additional fertilizer nitrogen. Most of the grassland nitrogen is immobilized in the soil as organic nitrogen in living tissue and nonliving detritus. Grassland soils in the Northern Plains contain about 3 to 8 tons of organic nitrogen per acre. Soil organic nitrogen must be converted into mineral nitrogen through mineralization by soil microorganisms in order to be available to grassland plants. The greater the biomass of soil microorganisms, the greater the quantity of available mineral nitrogen.

Rangelands managed by the twice-over rotation grazing strategy are not deficient in available mineral nitrogen. The biologically effective twice-over rotation grazing management strategy is designed to use partial defoliation of grass tillers at beneficial phenological growth stages to meet the biological requirements of grassland plants and to stimulate rhizosphere organism activity that enhances the biogeochemical processes in grassland ecosystems and increases the quantity of organic nitrogen mineralized into inorganic (mineral) nitrogen at amounts sufficient for herbage production at maximum potential yield levels (Manske 2007).

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Literature Cited

Goetz, H. 1969. Composition and yields of native grassland sites fertilized at different rates of nitrogen. Journal of Range Management 22:384-390.

Goetz, H. 1975. Availability of nitrogen and other nutrients on four fertilized range sites during the active growing season. Journal of Range Management 28:305-310.

Goetz, H., P.E. Nyren, and D.E. Williams. 1978. Implications of fertilizers in plant community dynamics of Northern Great Plains rangelands. Proceedings of the First International Rangeland Congress. p. 671-674.

Lorenz, R.J., and G.A. Rogler. 1972. Forage production and botanical composition of mixed prairie as influenced by nitrogen and phosphorus fertilization. Agronomy Journal 64:244-249.

Manske, L.L. 2007. Biology of defoliation by grazing. NDSU Dickinson Research Extension Center. Range Management Report DREC 09-1067. Dickinson, ND. 25p.

Manske, L.L. 2009a. Evaluation of plant species shift on fertilized native rangeland. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1071. Dickinson, ND. 23p.

Manske, L.L. 2009b. Cost of herbage weight for nitrogen fertilization treatments on native rangeland. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1072. Dickinson, ND. 10p.

Power, J.F., and J. Alessi. 1971. Nitrogen fertilization of semiarid grasslands: plant growth and soil mineral N levels. Agronomy Journal 63:277-280.

Rogler, G.A., and R.J. Lorenz. 1957. Nitrogen fertilization of Northern Great Plains rangelands. Journal of Range Management 10:156-160.

Smika, D.E., H.J. Haas, and J.F. Power. 1965. Effects of moisture and nitrogen fertilizer on growth and water use by native grass. Agronomy Journal 57:483-486.

Taylor, J.E. 1976. Long-term responses of mixed prairie rangeland to nitrogen fertilization and range pitting. Ph.D. Thesis, North Dakota State University, Fargo, ND. 97p.

Whitman, W.C. 1957. Influence of nitrogen fertilizer on native grass production. Annual Report. Dickinson Experiment Station. Dickinson, ND. p. 16-18.

Whitman, W.C. 1963. Fertilizer on native grass. Annual Report. Dickinson Experiment Station. Dickinson, ND. p. 28-34.

Whitman, W.C. 1976. Native range fertilization and interseeding studies. Annual Report. Dickinson Experiment Station. Dickinson, ND. p. 11-17.

Whitman, W.C. 1978. Fertilization of native mixed prairie in western North Dakota. Annual Report. Dickinson Experiment Station. Dickinson, ND. p. 20-22.

Wight, J.R., and A.L. Black. 1972. Energy fixation and precipitation use efficiency in a fertilized rangeland ecosystem of the Northern Great Plains. Journal of Range Management 25:376-380.

Wight, J.R., and A.L. Black. 1979. Range fertilization: plant response and water use. Journal of Range Management 32:345-349.

Biologically Effective Grazing Management Reduces the Detrimental Effects from Drought Conditions on Grasslands

Report DREC 11-3049b
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Healthy grassland ecosystems with fully functional biological and ecological processes are effected less from the negative impacts of drought conditions than moderate and low health status grassland ecosystems functioning at below potential levels. Biogeochemical processes of grassland ecosystems can be enhanced and biological requirements of grass plants can be met when partial defoliation by grazing occurs during phenological growth between the three and a half new leaf stage and the flowering (anthesis) stage activating compensatory physiological processes in remaining leaf and shoot tissue, stimulating vegetative reproduction from axillary buds, and stimulating rhizosphere organism activity that increases available mineral nitrogen (Manske 2007). Implementation of biologically effective grazing management during nondrought growing seasons improves the health status of grassland ecosystems (Manske 2001) and increases the resistance to detrimental effects from drought conditions.

Periods with rainfall shortage are normal weather conditions for the Northern Plains. Growing seasons with drought conditions occur during 15.3% of the years, or about 2 drought seasons every 13 years. Moderate drought conditions, that have growing season precipitation at less than 75% and greater than 50% of the long-term mean, occur during 11.9% of the years, or about 1 moderate drought in 8 years. Severe drought conditions, that have growing season precipitation at less than 50% of the long-term mean similar to the water deficiencies received in 1919, 1934, 1936, and 1988, occur during 3.4% of the years, or about 1 severe drought in 29 years. Nondrought conditions are an abnormal phenomenon and occur during only 5.9% of the growing seasons, or about 1 season without water deficiency in 17 years (Manske 2010a).

The average 6 month perennial plant growing season, mid April to mid October, has water deficiency or drought conditions during 2 of those months, 32.7%. The frequency of water deficiency occurrence is not distributed evenly across the growing season months. Water deficiency frequency has been 16.9% in April, 13.6% in May, 10.2% in June, 38.1% in July, 52.5% in August, 50.0% in September, and 46.6% in October (Manske 2010a).

Drought conditions reoccur at irregular intervals and can create serious forage deficiency problems for livestock producers. The precipitation shortage during drought conditions is generally assumed to be the sole cause for the reduction in herbage production and for the accompanying calamities. Because rainfall can not be increased on demand, it is commonly presumed that nothing can be done ahead of a drought to mitigate the detrimental impacts and it is consequently concluded that there is no other recourse than to improvise high-cost, makeshift, emergency schemes to get through the climatic hard times. Despite these common assumptions, by implementation of drought mitigating management practices, drought conditions do not have to be reoccurring disasters.

Low rainfall is the most obvious detrimental factor occurring during a drought, however, there are additional factors involved that intensify the severity of the problems that develop during drought conditions. Along with low precipitation, high evapotranspiration rates and antagonistic effects from the previous years' traditional grazing management practices that reduce grass plant size and density, decrease soil organism activity, deteriorate soil structure, and reduce ecosystem health status negatively affect the quantity of herbage produced during drought conditions. The detrimental effects caused by these additional factors can be diminished by implementing biologically effective grazing management strategies that increase grass plant size and density, stimulate rhizosphere organism activity, improve soil structure, and increase ecosystem health status.

The shortage of rainfall should not be given all of the blame for all the problems that materialize during drought conditions. If reduced rainfall was the only factor causing reduced herbage production, the percent reduction in herbage below normal herbage production would be the same as the percent reduction in precipitation. Herbage production on grasslands managed with traditional grazing management practices is usually reduced by about double the percent reduction in precipitation. During the growing season of 2002, southcentral North Dakota received precipitation at 21% to 26% below normal. Most of the informed estimations in the reductions of herbage production were around 50% to 60% below normal (Manske 2002a, b).

The cause for the quantity of reduction in herbage production greater than the reduction in precipitation is primarily the reduction in available mineral nitrogen resulting from the detrimental effects of previous management practices. Traditional management practices, like seasonlong, deferred, and repeat seasonal grazing, are antagonistic to the processes that convert organic nitrogen into inorganic (mineral) nitrogen. A minimum rate of mineralization that supplies 100 pounds of mineral nitrogen per acre is required to sustain herbage production at biological potential levels on rangelands (Wight and Black 1972).

Wight and Black (1972) found that precipitation use efficiency (pounds of herbage production per inch of precipitation received) of rangeland grasses improved when soil mineral nitrogen was available at quantities greater than 100 lbs/ac. The inhibitory deficiencies of mineral nitrogen on rangelands that had less than 100 lbs/ac of available soil mineral nitrogen caused the weight of herbage production per inch of precipitation recieved to be reduced an average of 49.6% below the weight of herbage produced per inch of precipitation on the rangeland ecosystems that had greater than 100 lbs/ac of mineral nitrogen and did not have mineral nitrogen deficiencies (Wight and Black 1979). The quantity of herbage biomass production on rangeland ecosystems that have greater than 100 lbs/ac soil mineral nitrogen will be about double the quantity of herbage biomass production on rangeland ecosystems that have less than 100 lbs/ac soil mineral nitrogen, even during periods of water deficiency.

Manske (2010b, 2010c) found evidence that two defoliation resistance mechanisms had threshold requirements for activation at 100 lbs/ac of mineral nitrogen. Partial defoliation of grass tillers at phenological growth stages between the three and a half new leaf stage and the flower (anthesis) stage activated the compensatory physiological processes within grass plants that enabled partially defoliated grass tillers to rapidly and completely replace the leaf material removed by grazing, and activated the asexual processes of vegetative reproduction that produced secondary tillers from axillary buds in rangeland ecosystems that had soil mineral nitrogen available at quantities greater than 100 lbs/ac, however, the same defoliation treatments did not activate the defoliation resistance mechanisms of grass plants in rangeland ecosystems that had soil mineral nitrogen available at quantities less than 100 lbs/ac. Inhibitory mineral nitrogen deficiencies exist in rangeland ecosystems that have soil mineral nitrogen available at less than 100 lbs/ac and mineral nitrogen deficiencies do not occur in rangeland ecosystems that have soil mineral nitrogen available at 100 lbs/ac or greater.

The quantity of mineral nitrogen available on rangeland ecosystems managed by traditional grazing practices was found to be; 31.2 lbs/ac on deferred grazing, 62.0 lbs/ac on 6.0-m seasonlong, and 76.7 lbs/ac on 4.5-m seasonlong (figure 1).

Reductions in mineral nitrogen limit herbage production more often than water in temperate grasslands (Tilman 1990). Traditionally managed grasslands have below normal available mineral nitrogen and reduced herbage production even during nondrought growing seasons. Both low mineral nitrogen and low soil water are major factors that cause reductions in herbage production during drought conditions.

Grasslands in the Northern Plains are not low in nitrogen. Grassland soils contain about 3 to 8 tons of organic nitrogen per acre. Plants, however, can not use organic nitrogen. The organic nitrogen must be converted into mineral nitrogen to be usable by plants. Soil microorganisms in the rhizosphere zone around perennial grass roots convert organic nitrogen into mineral nitrogen. This process is symbiotic and mutually beneficial for both the plants and the rhizosphere organisms. Plants fix carbon and capture energy from the sun during photosynthesis. Organisms in the rhizosphere are low in carbon and receive a portion of the carbon fixed by the plants. Grassland plants are low in mineral nitrogen which is a waste product from rhizosphere organism metabolism. Plants trade carbon to rhizosphere organisms for nitrogen and rhizosphere organisms trade nitrogen to plants for carbon (Manske 2007).

The quantity of organic nitrogen converted into mineral nitrogen by rhizosphere organisms is dependent on the quantity of carbon released into the rhizosphere by plants. The quantity of carbon released by the plants is dependent on the type of grazing management practices used and the amount of leaf material removed by grazing at different plant phenological growth stages. Traditional grazing management practices that are not based on the biological requirements and the phenological growth stages of plants suppress the quantity of carbon released into the rhizosphere causing a reduction in rhizosphere organism volume and activity, resulting in a reduction in the quantity of available mineral nitrogen. The quantity of available mineral nitrogen gradually decreases each year. After several years of management with traditional grazing practices, the accumulated reduction in rhizosphere volume and in available mineral nitrogen results in a substantial reduction in herbage biomass production at about 50% to 75% of the grasslands' potential herbage biomass production (Manske 2007). The traditional grazing management practices of 6.0-month seasonlong and 4.5-month seasonlong caused decreases of 78.1% and 70.2% in rhizosphere volume after 20 years of treatment, respectively (figure 1) (Manske 2008). During growing seasons with drought conditions, both mineral nitrogen and soil water are greatly diminished in grasslands managed with traditional grazing practices and are the two major causes for reductions in herbage production and the resulting reductions in stocking rate.

The biologically effective twice-over rotation grazing management strategy that is based on partial defoliation at beneficial phenological growth stages and on meeting the biological requirements of grass plants enhanced the biogeochemical processes in grassland ecosystems and caused a 131.8% increase in available mineral nitrogen after six years of treatment and caused a 235.8% increase in rhizosphere volume after 20 years of treatment greater than that on 4.5-month seasonlong (figure 1) (Manske 2008). Biologically effective grazing management improves the health status of grassland ecosystems increasing the ecosystems resistance to drought conditions. The increased rhizosphere organism volume and activity increases the quantity of available mineral nitrogen. The increased ectomycorrhizal fungi in the rhizosphere improves the structure of the soil by increasing the quantity and depth of aggregation which increases the quantity of water infiltration and increases the water holding capacity of the soil. The increased plant density and increased litter cover shade the soil, lowering the soil temperature and decreasing the rate of soil water loss through evaporation (Manske 2007). During growing seasons with drought conditions, the mineral nitrogen and soil water are not reduced as severely and the quantity of herbage biomass production is not reduced as greatly on grasslands managed with the twice-over rotation strategy as those on grasslands managed with traditional grazing practices.

The quantities of soil water and mineral nitrogen available for grassland plants affect the quantity of herbage biomass production and the stocking rates during growing seasons with drought conditions and affect the length of time needed for recovery after droughts. Recovery of grasslands managed with heavily stocked traditional grazing practices following the severe drought conditions of 1936, that had growing season precipitation at less than 50% of the long-term mean (Manske 2010a), required 4 years with greatly reduced stocking rates (Whitman et al. 1943). Grasslands managed with moderately stocked traditional seasonlong grazing practices required 2 years with reduced stocking rates to recover; and grasslands managed with the biologically effective twice-over rotation grazing strategy required 1 year with only slightly reduced stocking rates to recover following the severe drought conditions of 1988 (Manske 1989, 1990), that had growing season precipitation at less than 50% of the long-term mean (Manske 2010a). Recovery following growing seasons with moderate drought conditions, that have below normal precipitation at greater than 50% but less than 100% of the long-term mean and with perennial grasses under water stress for 2.5 to 3.5 months, required 1 year with reduced stocking rates for grasslands managed with moderately stocked traditional seasonlong grazing practices, and required less than 1 growing season with no reductions in stocking rates for grasslands managed with the twice-over rotation grazing strategy (Manske, data on file).

Healthy grasslands managed with biologically effective grazing practices have lower reductions in herbage biomass production during droughts and require less recovery time after droughts than moderately healthy grasslands managed with moderately stocked traditional grazing practices, which in turn, have lower reductions in herbage biomass production during droughts and require less recovery time after droughts than grasslands possessing low health status managed with heavily stocked traditional grazing practices (table 1) (Whitman et al. 1943; Manske 1989, 1990).

During a hypothetical 48 year career in agriculture (table 1), a beef producer in the Northern Plains experiences 3 growing seasons with no drought conditions, 37 growing seasons each with an average of 2 months with water deficiencies, 6 growing seasons with moderate drought conditions that have precipitation at less than 75% but greater than 50% of the long-term mean, and 2 growing seasons with severe drought conditions that have precipitation at less than 50% of the long-term mean. The degree of reductive impacts on grassland herbage production and stocking rates encountered during drought conditions depends on the level of effectiveness that the previous grazing management has benefited the grass plant biological requirements and the ecosystems biogeochemical processes. The number of years with reduced herbage production and reduced stocking rates resulting from drought conditions and recovery from drought conditions as affected by the managed health status of grassland ecosystems are shown in table 1.

Grasslands with low health status (available mineral nitrogen at less than 50 lbs/ac) managed by heavy stocking or by starting dates too early and/or ending dates too late with traditional grazing practices have reduced herbage production and reduced stocking rates during 6 growing seasons with moderate drought conditions and 2 growing seasons with severe drought conditions. Low health status grasslands require 2 years of recovery with reduced stocking rates for moderate drought conditions and 4 years of recovery with greatly reduced stocking rates for severe drought conditions resulting in a total of 28 years (58.3%) with reduced herbage production and reduced stocking rates; 8 years caused by drought conditions and 20 years caused by recovery from drought conditions. Low health status grasslands are properly stocked at full capacity for 20 years (41.7%) (table 1).

Grasslands with moderate health status (available mineral nitrogen between 50 and 75 lbs/ac) managed with moderately stocked traditional grazing practices have reduced herbage production and reduced stocking rates during 6 growing seasons with moderate drought conditions and 2 growing seasons with severe drought conditions. Moderate health status grasslands require 1 year of recovery with reduced stocking rates for moderate drought conditions and 2 years of recovery with reduced stocking rates for severe drought conditions resulting in a total of 18 years (37.5%) with reduced herbage production and reduced stocking rates; 8 years caused by drought conditions and 10 years caused by recovery from drought conditions. Moderate health status grasslands are properly stocked at full capacity for 30 years (62.5%) (table 1).

Grasslands with high health status (available mineral nitrogen greater than 100 lbs/ac) managed with biologically effective twice-over rotation grazing strategies have some reduction in herbage production, but the stocking rate is not reduced, during 6 growing seasons with moderate drought conditions; and high health status grasslands have reduced herbage production and reduced stocking rates during 2 growing seasons with severe drought conditions. High health status grasslands have sufficient resistance to moderate drought conditions that reduction in stocking rate is not necessary during 1 season of moderate drought, however, if 2 growing seasons with moderate drought conditions occur successively, stocking rates need to be reduced during the second season. High health status grasslands require less than 1 growing season with no reduction in stocking rates to recover from moderate drought conditions and require 1 year with reduced stocking rates to recover from severe drought conditions resulting in a total of 4 years (8.3%) with reduced herbage production and reduced stocking rates; 2 years caused by drought conditions and 2 years caused by recovery from drought conditions. High health status grasslands are properly stocked at full capacity for 44 years (91.7%) (table 1).

With a frequency of drought conditions occurring during an average of 15.3% of the years in the Northern Plains, it is necessary to reduce stocking rates during 58.3% of the years (28) on grasslands at low health status, 37.5% of the years (18) on grasslands at moderate health status, and 8.3% of the years (4) on grasslands at high health status. The number of years during a beef producers career that grasslands have reduced herbage production and reduced stocking rates resulting from drought conditions and recovery from drought conditions is related to the managed health status of the ecosystem. Biologically effective grazing management based on meeting the biological requirements of grass plants and on enhancing the biogeochemical processes of ecosystems improves the health status of the grassland and reduces the negative impacts from drought conditions.

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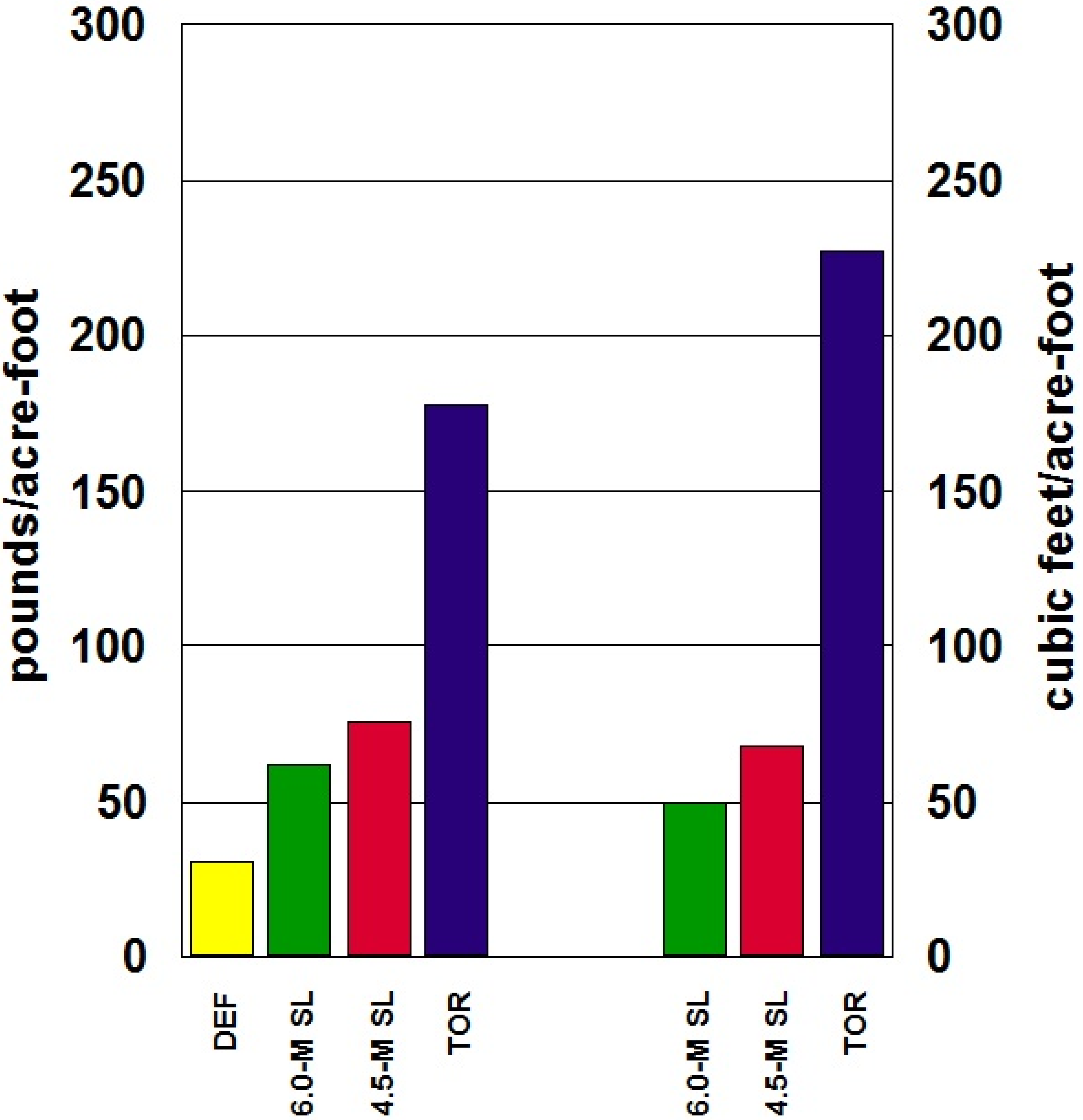

Mineral nitrogen (pounds/acre-foot) and rhizosphere volume (cubic feet/acre-foot) for grazing management treatments.

Table 1. Effects from drought conditions and length of recovery time on the number of years with reduced stocking rates on grasslands with different managed health status.

Ecosystem Health Status			Healthy Grasslands	Moderately Healthy Grasslands	Low Health Grasslands
Available Soil Mineral Nitrogen			>100 lbs/ac	50-75 lbs/ac	<50 lbs/ac
Ag Career		yrs	48	48	48
No Drought	(5.9%)	yrs	3	3	3
Drought for 2 mo/yr	(78.8%)	yrs	37	37	37
Moderate Drought Growing Seasons	(11.9%)	yrs	6	6	6
Recovery Time		yrs	0	6	12
Severe Drought 1936-1988 levels	(3.4%)	yrs	2	2	2
Recovery Time		yrs	2	4	8
Reduced Stocking for Droughts		yrs	2	8	8
Reduced Stocking for Recovery Time		yrs	2	10	20
Total Time with Reduced Stocking		yrs	4	18	28
Fully Stocked		yrs	44	30	20

Drought frequency data from Manske 2010a.
Recovery time data from Whitman et al. 1943 and Manske 1989, 1990.

Literature Cited

Manske, L.L. 1989. The drought of the 1980's compared to the drought of the 1930's and grazing management recommendations. NDSU Extension Service. Video Tape Presentation. Fargo, ND.

Manske, L.L. 1990. North Dakota rangeland changes similar to 1930's. NDSU Extension Service News Release. February. Fargo, ND. 3p.

Manske L.L. 2001. Grassland ecosystem monitoring: A nonquantitative procedure for assessing rangeland performance status. NDSU Dickinson Research Extension Center. Range Mangement Report DREC 01-1034. Dickinson, ND. 16p.

Manske, L.L. 2002a. Healthy plants have smaller forage reductions during precipitation shortages. NDSU Extension Service News Release. August. Fargo, ND. 3p.

Manske, L.L. 2002b. Management practices contributed to last summer's herbage reductions. NDSU Extension Service News Release. December. Fargo, ND. 2p.

Manske, L.L. 2007. Biology of defoliation by grazing. NDSU Dickinson Research Extension Center. Range Management Report DREC 07-1067. Dickinson, ND. 25p.

Manske, L.L. 2008. Grazing and burning treatment effects on soil mineral nitrogen and rhizosphere volume. NDSU Dickinson Research Extension Center. Range Research Report DREC 08-1066b. Dickinson, ND. 15p.

Manske, L.L. 2010a. Environmental factors to consider during planning of management for range plants in the Dickinson, North Dakota, region, 1892-2009. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1018m. Dickinson, ND. 37p.

Manske, L.L. 2010b. Leaf stage development of western wheatgrass tillers. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1075. Dickinson, ND. 48p.

Manske, L.L. 2010c. Evaluation of the defoliation resistance mechanisms influence on vegetative tiller initiation and tiller density. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1076. Dickinson, ND. 13p.

Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58:3-15.

Whitman, W., H.C. Hanson, and R. Peterson. 1943. Relations of drought and grazing to North Dakota range lands. North Dakota Agricultural Experiment Station Bulletin 320. Fargo, ND. 29p.

Wight, J.R., and A.L. Black. 1972. Energy fixation and precipitation use efficiency in a fertilized rangeland ecosystem of the Northern Great Plains. Journal of Range Management 25:376-380.

Wight, J.R., and A.L. Black. 1979. Range fertilization: plant response and water use. Journal of Range Management 32:345-349.

Effects from prescribed burning treatments on mixed grass prairie

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Introduction

Restoration of degraded grassland ecosystems requires the reactivation of the complex biological and ecological processes within native plants and within the rhizosphere organisms that convert soil organic nitrogen into inorganic nitrogen.

The primary cause of deterioration in grassland ecosystems is management practices that are antagonistic to the rhizosphere organism population. Decreases in rhizosphere organism biomass result in reductions in the quantity of organic nitrogen converted into inorganic nitrogen; this conversion is one of the primary functions of rhizosphere organisms. Decreases in the amount of inorganic nitrogen in an ecosystem cause reductions in grass biomass production and decreased native plant density (basal cover), creating larger and more numerous bare spaces between grass plants. These open spaces in the plant community provide ideal habitat for growth of opportunistic "weedy" plant species that are not dependent on the nitrogen converted by rhizosphere organisms. Once established, most opportunistic weedy species have mechanisms that aid in widening the species' distribution; the spread of the weeds indicate further degradation of the grassland ecosystem.

Additions of mineral (inorganic) nitrogen fertilizers to native grassland soils are antagonistic to rhizosphere organism populations, causing greater ecosystem degradation and pushing the plant species composition to be dominated by domesticated cool-season grasses like smooth bromegrass, crested wheatgrass, and Kentucky bluegrass. Other "quick fix" practices that treat only symptoms of the problem and do not correct the cause of the problem also result in further degradation of the ecosystem.

The solution for restoration of degraded grassland ecosystems is to correct the cause of the problem rather than just treat the symptoms of the problem. Grazing management coordinated with grass plant phenological development has been shown to stimulate rhizosphere organism increases in biomass and activity levels (Gorder, Manske, and Stroh 2004, Manske 2005), resulting in increased quantities of inorganic nitrogen (Coleman et al. 1983).

This study was conducted to investigate the possibilities of using prescribed burning treatments in the restoration of degraded mixed grass prairie ecosystems.

Study Area

The study area was the Lostwood National Wildlife Refuge, located in Burke and Mountrail counties in northwestern North Dakota between 48° 50' and 48° 30' north latitude and 102° 40' and 102° 20' west longitude. The landscape is glacial terminal moraine of the Missouri Coteau. Topography is rolling to steep hills interspersed with shallow lakes and prairie wetlands. Soils are primarily fine-loamy, mixed Typic Haploboralls and fine-loamy, mixed Typic Argiboralls. Some areas have sandy or gravelly substratum. Native vegetation is the Wheatgrass-Needlegrass Type (Barker and Whitman 1988) of the mixed grass prairie.

The region was homesteaded between 1910 and 1930. During that period, about 25% of the upland was plowed and used as cropland. Most likely, grazing livestock had access to the remainder of the area. Naturalists' surveys of the region conducted in 1913-1915 described one lone grove of trees located at the southeastern corner of the refuge's lower long lake (Smith 1997). The trees were cut down for their wood, and the lake became known as lower Lostwood Lake.

Because of economic troubles of the time, the federal government developed relief programs to repurchase failed homestead land during the mid to late 1930's. The homestead acres repurchased under land utilization projects were designated for three specific purposes. The acres identified for grazing use and economic development from livestock agriculture became the Little Missouri National Grasslands, acres identified for recreational use became Theodore Roosevelt National Park, and acres identified for wildlife use became Lostwood National Wildlife Refuge.

The Lostwood Wildlife Refuge consists of 26,904 acres (10,896 ha) with 5,381 acres (2,179 ha) of wetlands and 5,577 acres (2,259 ha) of wilderness (Smith 1997). Early management of the refuge was based on the concept of preserving wildlife habitat with little or no disturbance (idle), and about 15% of the refuge has never been burned, grazed, or mowed.

All grazing on the refuge was stopped between 1935 and 1940. After 1940, about 59% of the refuge was grazed periodically using deferred seasonlong management with some areas grazed only one time and other areas grazed as many as 22 times over a 35-year period. Between 1940 and 1975, about 26% of the refuge was annually grazed with seasonlong management for 4.5 to 5.0 months at low to moderate stocking rates, primarily during July through November (Smith 1988). This deferred-type management that delays grazing until after the flowering stage of grasses is known to decrease grass tiller density (Sarvis 1941, Manske et al. 1988).

After 1935, some of the land parcels previously used as cropland by homesteaders (about 8% of the refuge) were allowed to "go back" by natural revegetation through secondary succession. The remaining cropland parcels were managed as cropland until the mid 1950's, when about 15% of the refuge was reseeded with domesticated cool-season grasses, primarily smooth bromegrass and crested wheatgrass (Smith 1988).

The available records indicate that the inhabitants of the region had suppressed all fires from sometime in the late 1800's and that refuge land had not been burned in over 80 years by wildfire or prescribed fire until a prescribed burning program was started in 1978 (Smith 1985b).

There were few trees on the refuge during the 1930's and 1940's, but by 1985, there were over 540 expanding aspen groves covering about 475 acres (192 ha) interspersed across the landscape located at the edges of seasonal wetlands, with about 300 aspen groves completely occupying previous wetland basins (Smith 1997).

The shrub cover on Lostwood Wildlife Refuge increased from about 5% during the mid 1930's to greater than 50% in 1979. This change, however, did not occur at a uniform rate. The shrub composition in the plant community did not change much during the first 20 years. A substantial increase in shrub cover occurred between 1953 and 1969 and, between 1969 and 1979, the western snowberry colonies expanded rapidly and invaded extensive areas of degraded grassland; as a result, over half of the refuge upland was transformed into shrubland (Smith 1988). Kentucky bluegrass was the dominant grass associated with the western snowberry colonies. Large portions of the western snowberry colonies were extremely dense and had no herbaceous understory. Decadent centers of old western snowberry colonies had been reinvaded by smooth bromegrass, quackgrass (Smith 1985a), and Canada thistle (Smith 1985b.). Native grasses and forbs were still present in low quantities in some areas but were greatly suppressed.

Refuge manager Karen Smith initiated an every-other-year prescribed burning strategy that was conducted from 1978 to 2002. The every-other-year burn regime was designed to reduce the invading western snowberry and exotic grasses and renovate the prairie ecosystem. Annual burns were not possible because of insufficient production of plant biomass for fuel (Smith 1985a). The refuge was subdivided into prescribed burn management units that used trails or mowed swaths as fire breaks. Several parcels of the refuge received no burning treatments and were used as reference control areas. The prescribed burns were conducted during four seasons: early spring (mid-late April), 1 replication; spring (May-mid June), 3 replications; early summer (mid June-July), 7 replications; and mid summer (early-mid August), 4 replications. The number of repeated every-other-year burns was 1 burn, 4 replications; 2 burns, 4 replications; 3 burns, 4 replications; and 4 burns, 3 replications. Control treatments, 6 replications, had no burning (wildfires or prescribed burns) for over 100 years, since sometime during the late 1800's. In 1990, Manske (1992) evaluated the effects of every-other-year prescribed burning after thirteen years of treatments (1978-1990). This report is a summary of that study.

Procedures

Field data were collected on permanent landscape transects that included the plant communities on the summit, shoulder, back, foot, and toe slopes from 15 prescribed burn management units with an average size of 530.5 acres (214.85 ha) and 6 control management units of no burning with an average size of 436.8 acres (176.90 ha). A standard paired plot t-test was used to analyze differences between means (Mosteller and Rourke 1973).

Aboveground herbage biomass was collected during peak growth in mid to late July by the standard clipping method (Cook and Stubbendieck 1986). The herbage material from three 0.25 m^2 quadrats (frames) located along the landscape transects for each treatment was sorted in the field by biotype categories: grasses, sedges, forbs, shrubs, and standing dead. The herbage of each biotype category from each frame was placed in labeled paper bags of known weight, oven dried at 176° F (80° C), and weighed.

Plant species composition was determined during peak growth, between mid July and mid August, by the plant shoot cover method (% shoot frequency) (Cook and Stubbendieck 1986), with one hundred 0.1 m^2 quadrats placed systematically along the landscape transects of each treatment.

Endomycorrhizal fungal infection in roots was evaluated for blue grama, western wheatgrass, smooth bromegrass, and western snowberry. Three replicated soil cores 4 inches (10.2 cm) in diameter and 4 inches (10.2 cm) in depth were collected for each of the four plant species; samples from nearly level loam soils along the permanent landscape transects of each control and prescribed burn treatment were taken with a golf cup cutter. Roots were washed over sieving, and current year's roots were removed from plant crowns by clipping. Root samples of each replicate were stored in individual vials and preserved in a solution of glycerin and lactic acid. In the laboratory, root samples were cleared and stained to enhance mycorrhizal structures using procedures described by Phillips and Hayman (1970) and modified by Kormanik and McGraw (1982). Fungal colonization in the root samples was scanned through a Nikon 107733 type 104 microscope, and percent fungal infection was assessed using a nonsystematic modification of the grid-intersect method (Giovannetti and Mosse 1980), with presence or absence (P/A) of fungal structures recorded for 100 intersected root segments.

Changes in soil microorganism activity were monitored by change in the quantity of soil inorganic (mineral) nitrogen in July and August. Five replicated soil cores 1 inch (2.54 cm) in diameter and 6 inches (15.24 cm) in depth were collected from nearly level loam soils along the permanent landscape transects of each control and prescribed burn treatment and air dried. In the laboratory, subsamples of the soil cores were evaluated for total incubated mineralizable nitrogen (N) with procedures outlined by Keeney (1982). Inorganic forms of nitrogen were extracted from soil samples by adding a reagent, 2 M KCl, at the rate of 50 ml/10 g of soil; samples were then shaken for one hour. The extract was analyzed for ammonium (NH_4) and nitrate (NO_3) by steam distillation (Keeney and Nelson 1982). Soil nitrite (NO_2) was not analyzed because it is seldom present in detectable quantities and no methods had been developed that were adequately sensitive to obtain reliable estimates of nitrite.

Gravimetric soil water data (Cook and Stubbendieck 1986) were collected on both the summit slopes and foot slopes of each landscape transect in July and August using a 1-inch (2.54 cm) Veihmeyer soil tube at depths of 0-6, 6-12, and 12-24 inches (0-15.24, 15.24-30.48, and 30.48-60.96 cm) and oven dried at 212° F (100° C). Weather data for the region were collected at the Des Lacs NWR weather station.

Results

The Lostwood Wildlife Refuge region has cold winters and hot summers typical of continental climates. January was the coldest month, and July and August were the warmest months. Plants experience temperature stress during months with mean monthly temperatures below 32.0° F (0.0° C). From November through March each year, plants in northwestern North Dakota cannot conduct active growth because mean temperatures are below 32.0° F (0.0° C).

The long-term (1936-1989) annual precipitation at the Lostwood Wildlife Refuge region is 16.50 inches (419.10 mm). The growing-season precipitation (April through October) is 13.80 inches (350.52 mm), 83.64% of the annual precipitation. The seasonal period during which the greatest precipitation occurs is spring–April, May, and June–with 6.62 inches (168.15 mm), 40.12% of the annual precipitation. June has the greatest monthly precipitation, 3.32 inches (84.33 mm). The precipitation received during the 3-month period of May, June, and July accounts for 46.67% of the annual precipitation (7.70 inches, or 195.58 mm). The precipitation received during the 5-month period of November through March averages 2.70 inches (68.58 mm), 16.36% of the annual precipitation. The seasonal period during which the least precipitation occurs is winter–January, February, and March–with 1.69 inches (42.93 mm), 10.24% of the annual precipitation.

Annual precipitation during the study period (1978-1990) averaged 15.36 inches (390.14 mm), 93.10% of the long-term mean (LTM), and growing-season precipitation, April though October, averaged 12.35 inches (313.69 mm), 89.48% of the LTM growing-season precipitation (table 1). The growing-season precipitation was greater than the long-term mean during 1978, 1982, 1984, 1985, 1986, and 1990, and lower than the long-term mean during 1979, 1980, 1981, 1983, 1987, 1988, and 1989 (table 1). The growing-season precepitation during 1979, 1983, 1987, and 1988 was 48.2%, 62.2%, 60.2%, and 69.6% of the long-term mean, respectively (table 1). The water deficiencies during 1979, 1983, 1987, and 1988 caused water stress in perennial plants so that herbage biomass production in the region was restricted.

The quantity of soil water during the growing season (July and August), to 24 inches (60.96 cm) in depth, was not significantly different among the no burn control treatments and the number of repeated every-other-year burn treatments (table 2) and the seasonal period of every-other-year burn treatments (table 3).

The total current year's production of aboveground biomass was not different after one, two, three, and four repeated prescribed burns compared to the biomass of the unburned treatment (table 4). However, the composition of the aboveground biomass changed remarkably. The contribution of grasses to the total biomass changed from 24.2% on treatments with no burns to 65.6% after four burns (table 4), an increase of 171.1%. Grass biomass decreased 24.7% after one burn and increased 109.3% after four burns (table 4). The contribution from sedges changed from 13.2% on treatments with no burns to 11.1% after four burns. Sedge biomass increased 61.6% after one burn and decreased 35.1% after four burns (table 4). The contribution from forbs changed from 15.0% on treatments with no burns to 20.3% after four burns. After one burn, the forb contribution to total aboveground biomass was 139.7% greater than that on the unburned treatments. After two and three burns, the weedy forbs decreased and the ecological status of perennial forbs improved. The forb contribution to the total biomass production after four burns was 35.3% greater than that on the unburned treatments. Forb biomass increased 78.0% after one burn and increased 4.4% after four burns (table 4). The biomass contribution from shrubs changed from 47.5% on treatments with no burns to only 3.0% after four burns (table 4), a 93.7% decrease. Shrub biomass decreased 83.1% after one burn and decreased 95.1% after four burns (table 4).

Native grass shoot frequency increased significantly as a result of repeated burning. The average increase after one, two, and three burns was 79.6%; after four burns, native grass shoot frequency increased 94.7% (table 5). The quantity of basal cover area for native grasses, however, was not well developed even after four burns. Sedge shoot frequency increased an average of 58.4% after repeated burning. Introduced grass shoot frequency decreased an average of 49.4% after one, two, and three burns and decreased 65.1% after four burns. Four burns were required to reduce introduced grasses significantly (table 5). Kentucky bluegrass shoot frequency decreased an average of 36.2% after one, two, three, and four burns. Quackgrass shoot frequency decreased an average of 84.0% after one and two burns and decreased an average of 90.9% after three and four burns. Smooth bromegrass shoot frequency decreased an average of 90.0% after one and two burns and decreased an average of 96.7% after three and four burns.

Perennial forb shoot frequency increased 39.3% after one burn (table 5) and increased an average of 7.5% after additional repeated burns of two, three, and four times. Early succession and weedy forb shoot frequency increased 8.2% after one burn, decreased an average of 7.5% after two and three burns, and decreased 50.9% after four burns (table 5). Four burns were required to reduce weedy forbs significantly (table 5).

Shrub shoot frequency decreased 36.4% after one burn, decreased an average of 46.1% after two and three burns, and decreased 58.2% after four burns (table 5). Four burns were required to reduce shrubs significantly (table 5).

Western snowberry shoot frequency decreased 62.7% after one burn, decreased an average of 55.8% after two and three burns, and decreased 64.0% after four burns. Shoot frequency of western snowberry changed little from repeated burning after the first burn. However, the aboveground biomass produced by the shrubs was greatly reduced after the third and fourth burns.

All burns cause some damage to plants, but the seasonal period that prescribed burns are conducted affects the biomass production and shoot frequency of plant biotypes differently. Effective prescribed burns are conducted during appropriate seasonal periods so that the greatest reduction to the undesirable plants is caused and the damage to the desirable plants is minimized.

Grass biomass greatly increased after spring (May-mid June) and mid summer (early-mid August) burns but decreased after early summer (mid June-July) burns (table 6). Grass shoot frequency increased significantly after burns conducted during all seasonal periods. The greatest increases occurred after spring (May-mid June) and mid summer (early-mid August) burns (table 7). Shoot frequency of native cool-season grasses increased significantly after burns conducted during all seasonal periods (table 8). Shoot frequency of western wheatgrass increased significantly after early spring (mid-late April) burns and decreased after spring (May-mid June) burns (table 8). Shoot frequency of native warm-season grasses increased significantly after burns conducted during spring (May-mid June) (table 8). Blue grama shoot frequency increased significantly after spring (May-mid June) burns (table 8). Shoot frequency of introduced grasses decreased significantly after spring (May-mid June) burns (table 7). Kentucky bluegrass shoot frequency decreased significantly after spring (May-mid June) burns (table 8) and increased after early spring (mid-late April) burns (table 8). Smooth bromegrass and quackgrass shoot frequency decreased after burns conducted during all seasonal periods. Smooth bromegrass shoot frequency decreased most after early spring (mid-late April) burns (table 8). Quackgrass shoot frequency decreased most after spring (May-mid June) burns (table 8).

Sedge biomass increased after burns conducted during early spring (mid-late April) and early summer (mid June-July) and decreased after spring (May-mid June) and mid summer (early-mid August) burns (table 6). Shoot frequency of sedges increased significantly after spring (May-mid June) burns (table 7).

Forb biomass increased after burns conducted during all seasonal periods. The greatest increases occurred after early spring (mid-late April) and spring (May-mid June) burns (table 6). Shoot frequency of perennial forbs increased after early spring (mid-late April) and early summer (mid June-July) burns and decreased slightly after spring (May-mid June) burns (table 7). Shoot frequency of weedy forbs increased significantly after early spring (mid-late April) burns and decreased after spring (May-mid June), early summer (mid June-July), and mid summer (early-mid August) burns (table 7).

Shrub biomass decreased after burns conducted during all seasonal periods. The greatest decreases occurred after early spring (mid-late April), spring (May-mid June), and mid summer (early-mid August) burns (table 6). Shoot frequency of shrubs decreased significantly after early spring (mid-late April), spring (May-mid June), and mid summer (early-mid August) burns (table 7). Shrub shoot frequency did not decrease significantly after early summer (mid June-July) burns (table 7). Silverberry shoot frequency decreased significantly after early spring (mid-late April) and mid summer (early-mid August) burns (table 9). Western rose shoot frequency decreased significantly after early spring (mid-late April) and spring (May-mid June) burns (table 9) and increased slightly after early summer (mid June-July) and mid summer (early-mid August) burns. Shoot frequency of western snowberry decreased significantly after early spring (mid-late April), spring (May-mid June), and mid summer (early-mid August) burns (table 9). Western snowberry shoot frequency did not decrease significantly after early summer (mid June-July) burns (table 9).

Endomycorrhizal fungi do not colonize the entire root. Fungal colonization occurs at the portions of current year’s roots that are biologically active. Previous years’ roots, mature root portions, and young growing root portions do not host fungal structures. Percent fungal infection of root segments is primarily a factor of the proportion of biologically active root portions to the amount of mature and young root portions included in the sample. Identification of biologically active root portions from mature root portions is difficult in the field, with the naked eye or low-power hand lenses. Basically, the less than 100% fungal infection in the blue grama, western wheatgrass, and western snowberry root samples in tables 10 and 11 should be considered to indicate the percent biologically active root portions within the root sample. This evaluation, however, is not applicable to the smooth bromegrass root samples. Even though the smooth bromegrass root samples contained a small amount of young and mature root portions, most of the samples consisted of biologically active root portions and the percent fungal infection in tables 10 and 11 should be considered to be close to the percent fungal infection in smooth bromegrass samples. However, almost all of the fungal infection observed in the smooth bromegrass samples was restricted to the root hairs. Very few smooth bromegrass samples had fungal colonization within the root tissue. Even with the large differences in proportions of biologically active root portions within the root samples, the percent fungal infection in blue grama, western wheatgrass, and western snowberry root samples was significantly greater than the percent fungal infection in smooth bromegrass root samples on the number of repeated every-other-year prescribed burn treatments, the seasonal period of every-other-year prescribed burn treatments, and the control no burn treatments. Smooth bromegrass had virtually no fungal infection in the biologically active root tissue and relatively low fungal infection in the root hairs. The percent fungal infection in the roots of blue grama, western wheatgrass, western snowberry, and smooth bromegrass was not changed significantly by the number of repeated every-other-year prescribed burn treatments and the seasonal period of every-other-year prescribed burn treatments from the percent fungal infection in the respective plant species on the control no burn treatments (tables 10 and 11). The quantity of endomycorrhizal fungal colonization in plant roots was not stimulated by the prescribed burning treatments.

Grassland soils have abundant quantities of nitrogen; however, most of it is in the organic form and unavailable for direct use by plants. Grassland plants can use nitrogen only in the inorganic (mineral) form. Soil microorganisms of the rhizosphere convert soil organic nitrogen into inorganic nitrogen (Ingham et al. 1985). Grassland ecosystems with greater biomass of rhizosphere organisms convert greater quantities of organic nitrogen into inorganic nitrogen (Coleman et al. 1983). The quantities of inorganic nitrogen (NH_4-NO_3) in the soils on the number of repeated every-other-year prescribed burn treatments and the seasonal period of every-other-year prescribed burn treatments were not changed significantly from the quantities of inorganic nitrogen in the soils on the control no burn treatments (tables 10 and 11). The rhizosphere microorganism biomass and activity levels were not stimulated by the prescribed burning treatments, and the quantity of organic nitrogen converted into inorganic nitrogen was not stimulated by the prescribed burning treatments.

Discussion

Western snowberry aerial stems are sensitive to fire. The top growth is usually removed completely if sufficient fine fuel is present, and even if the stems are not completely consumed by the fire, they usually die to ground level. The belowground rhizomes and rhizome crowns with clusters of aerial stems are usually not damaged by fire. The belowground parts have large quantities of buds that have the potential to develop into new aerial sucker stems. Spring burns result in great quantities of sucker stems, which become visible about two weeks following the burn, and because carbohydrate stores can be completely replenished by the new plant material in one growing season, spring burns decrease shrub biomass but do not decrease stem frequency, even after numerous years of repeated burns. Prescribed burns conducted during early summer (mid June-July) cause the least reduction in western snowberry shoot frequency and shrub biomass production. These early summer burns coincide with western snowberry's major carbohydrate replenishment period, which occurs from full leaf expansion stage through most of the flowering stage, from early June to mid July.

Prescribed burns conducted during early spring (mid-late April), spring (May-mid June), and mid summer (early-mid August) result in decreased western snowberry shoot frequency and shrub biomass production. These burns coincide with the first two carbohydrate drawdown periods of western snowberry. The first carbohydrate drawdown period occurs during early spring, from mid April to early June (9 June), when the plants are in rapid growth to full leaf expansion stages. The second carbohydrate drawdown period occurs during the major portion of fruit fill stage, from mid July to mid August. Burns conducted during carbohydrate drawdown periods have greater success at western snowberry reduction than burns conducted during carbohydrate replenishment periods.

Kentucky bluegrass is increased by earlier burns and decreased by later spring burns. Weedy forbs are increased greatly by spring burns. However, four repeated burns conducted every-other-year significantly reduce the undesirable plants of introduced grasses, early succession and weedy forbs, and shrubs from mixed grass prairie habitat. Native grasses, sedges, and perennial forbs are not reduced by repeated every-other-year burning and benefit from the reduction in competition for sunlight from the taller shrubs.

Repeated every-other-year prescribed burning did not increase native grass basal cover (density), prescribed burning did not increase endomycorrhizal fungal infection of prairie plant roots, and prescribed burning did not increase the quantity of soil organic nitrogen converted into inorganic nitrogen. Stimulation of vegetative reproduction in grasses, stimulation of rhizosphere organism biomass and activity levels, and stimulation of biogeochemical cycling are the key physiological and ecological processes that grassland managers must activate in order to improve native plant health and vigor and to restore degraded ecosystems. Grassland fires do not improve mixed grass prairie ecosystems biologically or ecologically.

Historically, fire had been an environmental factor on mixed grass prairie, with an estimated fire return interval of 5 to 10 years on the moist regions and around 25 years on the dry regions (Wright and Bailey 1982, Bragg 1995). Most lightning-set fires occurred in July and August, and a large portion of the Indian-set fires occurred between July and early November (Higgins 1986). The Northern Plains mixed grass prairie has probably had considerably more late-season fires, occurring after mid July, than spring or early summer fires.

Spring burns during late April or May are severely detrimental to native cool-season grasses because of the removal of the valuable growth of the fall tillers and overwintering secondary tillers. June and early July burns are usually detrimental to native grass plants and hurt western snowberry plants only a little. Prescribed fire during August causes the least damage to native cool- and warm-season grasses and perennial forbs. An August fire removes all or most of the top growth of western snowberry and results in fewer sucker shoots the following year than a spring burn. August burns can be nearly nondetrimental to desirable plants when the soil is not dry, and August burns can cause considerable damage to the undesirable woody plants. Late April and May prescribed burns are less likely to escape control measures compared to August burns; however, the growth pattern and biological requirements of herbaceous vegetation in the mixed grass prairie match the August burns more closely (figure 1).

Conclusions

Grassland ecosystems in the mixed grass prairie degrade when managed with long-term idle (no defoliation) treatments and low to moderately stocked deferred grazing treatments. Ecosystem degradation does not occur at a uniform (linear) rate across time. The rate of decline begins slowly and accelerates progressively. The change in plant composition to greater abundance of nonrhizosphere species is basically a symptom, and the degree of plant species change lags behind the degree of ecosystem degradation.

Treatments that are designed to remove undesirable plant species do not restore ecosystem functions. Treatments that stimulate rhizosphere organism populations and enhance ecosystem biogeochemical cycles restore degraded grassland ecosystem processes; this restoration is followed by the improvement in plant composition to a greater abundance of rhizosphere species.

Prescribed burning can be used to kill western snowberry aerial stems to ground level and reduce shrub stem frequency, but fire alone will not eliminate western snowberry. Four repeated every-other-year burns can reduce introduced grasses, early succession and weedy forbs, and undesirable shrubs and woody plants.

Prescribed burning, however, cannot restore degraded grassland ecosystems because fire does not stimulate vegetative reproduction by tillering, a process that results in increased grass basal cover; fire does not stimulate endomycorrhizal fungal colonization of grass roots; fire does not stimulate rhizosphere organism biomass and activity levels; and fire does not stimulate conversion of soil organic nitrogen into inorganic nitrogen.

Acknowledgment

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Table 1. Precipitation in inches for growing-season months and the annual total precipitation for 1978-1990, Lostwood Wildlife Refuge, North Dakota.

	Apr	May	Jun	Jul	Aug	Sep	Oct	Growing Season	Annual Total
Long-term mean 1936-1989	1.28	2.02	3.32	2.36	1.94	1.87	1.01	13.80	16.50
1978	0.58	5.13	2.76	1.45	0.84	2.55	0.64	13.95	14.96
% of LTM	45.31	253.96	83.13	61.44	43.30	136.36	63.37	101.09	90.67
1979	1.59	1.75	0.61	1.32	0.04	0.84	0.50	6.65	8.72
% of LTM	124.22	86.63	18.37	55.93	2.06	44.92	49.50	48.19	52.85
1980	1.81	0.08	1.41	1.63	3.12	2.22	2.08	12.35	15.59
% of LTM	141.41	3.96	42.47	69.07	160.82	118.72	205.94	89.49	94.48
1981	0.41	0.50	4.06	2.77	2.71	1.31	0.65	12.41	15.34
% of LTM	32.03	24.75	122.29	117.37	139.69	70.05	64.36	89.93	92.97
1982	0.38	2.23	1.82	3.12	1.22	2.06	4.64	15.47	19.56
% of LTM	29.69	110.40	54.82	132.20	62.89	110.16	459.41	112.10	118.55
1983	0.19	1.30	1.44	2.42	1.37	1.04	0.82	8.58	12.19
% of LTM	14.84	64.36	43.37	102.54	70.62	55.61	81.19	62.17	73.88
1984	5.74	0.36	1.70	1.29	0.98	2.54	4.10	16.71	19.48
% of LTM	448.44	17.82	51.20	54.66	50.52	135.83	405.94	121.09	118.06
1985	0.69	4.77	1.81	0.99	3.98	2.07	1.60	15.91	18.40
% of LTM	53.91	236.14	54.52	41.95	205.15	110.70	158.42	115.29	111.52
1986	1.71	2.59	1.77	5.85	0.67	1.95	0.76	15.30	18.04
% of LTM	133.59	128.22	53.31	247.88	34.54	104.28	75.25	110.87	109.33
1987	0.10	1.80	0.89	3.83	0.73	0.66	0.30	8.31	12.16
% of LTM	7.81	89.11	26.81	162.29	37.63	35.29	29.70	60.22	73.70
1988	0.05	2.36	2.73	1.67	0.30	2.31	0.19	9.61	13.19
% of LTM	3.91	116.83	82.23	70.76	15.46	123.53	18.81	69.64	79.94
1989	0.70	1.30	3.31	2.66	0.80	1.59	0.48	10.84	16.37
% of LTM	54.69	64.36	99.70	112.71	41.24	85.03	47.52	78.55	99.21
1990	1.26	2.39	2.41	4.24	2.28	0.57	0.03	14.44	15.69
% of LTM	100.78	118.32	72.59	179.66	117.53	30.48	2.97	104.64	95.09
1978-1990	1.17	2.04	2.06	2.56	1.46	1.67	1.29	12.35	15.36
% of LTM	91.41	101.14	61.91	108.34	75.50	89.30	127.88	89.48	93.10

Table 2. Inches of soil water, 0-24 inches in depth, on summit and foot slopes with deep loam soils on the number of repeated every-other-year burn treatments.

	Depth in inches	No Burns 5 reps	One Burn 3 reps	Two Burns 3 reps	Three Burns 4 reps	Four burns 2 reps
Summit Slope						
July	0-24	3.00a	3.47a	3.11a	2.37a	2.53
August	0-24	2.31b	2.79b	2.17b	2.30b	2.35b
Foot Slope						
July	0-24	3.47c	3.47c	3.24c	2.88c	4.42c
August	0-24	2.58d	3.02d	2.45d	2.69d	3.35d

Data from Manske 1992
Means in the same row and followed by the same letter are not significantly different ($p<0.05$).

Table 3. Inches of soil water, 0-24 inches in depth, on summit and foot slopes with deep loam soils on the seasonal period of every-other-year burn treatments.

	Depth in inches	No Burns 5 reps	Early Spring (mid-late Apr) 1 rep	Spring (May-mid Jun) 1 rep	Early Summer (mid Jun-Jul) 6 reps	Mid Summer (early-mid Aug) 4 reps
Summit Slope						
July	0-24	3.00a	-	-	3.03a	2.94a
August	0-24	2.31b	2.30b	-	2.51b	2.56b
Foot Slope						
July	0-24	3.47c	-	-	3.36c	3.69c
August	0-24	2.58d	-	-	2.82d	3.01d

Data from Manske 1992
Means in the same row and followed by the same letter are not significantly different ($p<0.05$).

Table 4. Live biomass production of plant biotypes on the number of repeated every-other-year burn treatments and percent change from nonburned control.

Plant Biotypes		No Burns 6 reps	One Burn 4 reps	Two Burns 4 reps	Three Burns 4 reps	Four Burns 3 reps
Grass Biomass	(lbs/ac)	411.61a	310.12a	762.75a	512.87a	861.51a
% change	(%)		-24.7	85.3	24.6	109.3
Sedge Biomass	(lbs/ac)	224.59b	362.93b	74.34b	238.58b	145.81b
% change	(%)		61.6	-66.9	6.2	-35.1
Forb Biomass	(lbs/ac)	255.33c	454.35c	445.14c	587.41c	266.49c
% change	(%)		78.0	74.3	130.1	4.4
Shrub Biomass	(lbs/ac)	806.83d	136.00d	237.09d	52.00d	39.57d
% change	(%)		-83.1	-70.6	-93.6	-95.1
Total Live Biomass	(lbs/ac)	1698.36e	1263.39e	1519.19e	1390.87e	1313.38e
% change	(%)		-25.6	-10.6	-18.1	-22.7

Data from Manske 1992

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

Table 5. Shoot frequency of plant biotypes on the number of repeated every-other-year burn treatments and percent change from nonburned control.

Plant Biotypes		No Burns 6 reps	One Burn 4 reps	Two Burns 4 reps	Three Burns 4 reps	Four Burns 3 reps
Native Grass						
Shoot frequency	(%)	107.0a	194.3b	183.3ab	198.8b	208.3b
% change	(%)		81.6	71.3	85.8	94.7
Sedge						
Shoot frequency	(%)	56.7c	95.5d	97.0d	77.8cd	89.0cd
% change	(%)		68.4	71.1	37.2	57.0
Introduced Grass						
Shoot frequency	(%)	86.7e	46.3ef	31.8ef	53.5ef	30.3f
% change	(%)		-46.6	-63.3	-38.3	-65.1
Perennial Forbs						
Shoot frequency	(%)	120.5g	167.8h	125.5gh	137.5gh	125.7gh
% change	(%)		39.3	4.1	14.1	4.3
Weedy Forbs						
Shoot frequency	(%)	85.5i	92.5i	80.3ij	78.0ij	42.0j
% change	(%)		8.2	-6.1	-8.8	-50.9
Shrubs						
Shoot frequency	(%)	111.7k	71.0kl	58.5kl	62.0kl	46.7l
% change	(%)		-36.4	-47.6	-44.5	-58.2

Data from Manske 1992

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

Table 6. Live biomass production of plant biotypes on the seasonal period of every-other-year burn treatments and percent change from nonburned control.

Plant Biotypes		No Burns 6 reps	Early Spring (mid-late Apr) 1 rep	Spring (May-mid Jun) 3 reps	Early Summer (mid Jun-Jul) 7 reps	Mid Summer (early-mid Aug) 4 reps
Grass						
Biomass	(lbs/ac)	411.61a	571.59a	748.93a	347.88a	918.49a
% change	(%)		38.9	82.0	-15.5	123.1
Sedge						
Biomass	(lbs/ac)	224.59b	366.79b	48.88b	316.29b	103.33b
% change	(%)		63.3	-78.2	40.8	-54.0
Forb						
Biomass	(lbs/ac)	255.33c	771.40c	587.21c	451.17c	263.97c
% change	(%)		202.1	130.0	76.7	3.4
Shrub						
Biomass	(lbs/ac)	806.83d	0.0d	0.0d	226.43d	58.52d
% change	(%)		-100.0	-100.0	-71.9	-92.8
Total Live						
Biomass	(lbs/ac)	1698.36e	1709.78e	1385.02e	1341.77e	1344.18e
% change	(%)		0.7	-18.5	-21.0	-20.9

Data from Manske 1992

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

Table 7. Shoot frequency of plant biotypes on the seasonal period of every-other-year burn treatments and percent change from nonburned control.

Plant Biotypes		No Burns 6 reps	Early Spring (mid-late Apr) 1 rep	Spring (May-mid Jun) 3 reps	Early Summer (mid Jun-Jul) 7 reps	Mid Summer (early-mid Aug) 4 reps
Native Grass						
Shoot frequency	(%)	107.0a	189.0b	219.7b	182.9b	200.5b
% change	(%)		76.6	105.3	70.9	87.4
Sedge						
Shoot frequency	(%)	56.7c	39.0c	97.3d	93.4cd	90.8cd
% change	(%)		-31.2	71.6	64.7	60.1
Introduced Grass						
Shoot frequency	(%)	86.7e	73.0e	23.7f	43.4ef	42.3ef
% change	(%)		-15.8	-72.7	-49.9	-51.2
Perennial Forbs						
Shoot frequency	(%)	120.5g	157.0g	116.7g	154.6g	127.8g
% change	(%)		30.3	-3.2	28.3	6.1
Weedy Forbs						
Shoot frequency	(%)	85.5h	129.0i	43.3h	79.3h	78.8h
% change	(%)		50.9	-49.4	-7.3	-7.8
Shrubs						
Shoot frequency	(%)	111.7j	15.0l	22.0l	81.7jk	63.3k
% change	(%)		-86.6	-80.3	-26.9	-43.3

Data from Manske 1992

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

Table 8. Shoot frequency of grasses on the seasonal period of every-other-year burn treatments and percent change from nonburned control.

Plant Biotypes		No Burns 6 reps	Early Spring (mid-late Apr) 1 rep	Spring (May-mid Jun) 3 reps	Early Summer (mid Jun-Jul) 7 reps	Mid Summer (early-mid Aug) 4 reps
Native Grass						
Cool Season Grass						
Shoot frequency	(%)	89.2a	177.0b	166.0b	168.9b	169.0b
% change	(%)		98.4	86.1	89.3	89.5
Warm Season Grass						
Shoot frequency	(%)	17.8c	12.0c	53.7d	14.0c	31.5cd
% change	(%)		-32.7	201.0	-21.5	76.7
Western wheatgrass						
Shoot frequency	(%)	15.5e	42.0c	13.7e	16.4e	19.5e
% change	(%)		170.1	-11.8	6.0	25.8
Blue grama						
Shoot frequency	(%)	8.0f	4.0f	39.3g	7.4f	14.8fg
% change	(%)		-50.0	391.6	-7.1	84.4
Introduced Grass						
Smooth bromegrass						
Shoot frequency	(%)	17.5h	0.0h	2.3h	0.3h	2.3h
% change	(%)		-100.0	-86.7	-98.3	-87.1
Quackgrass						
Shoot frequency	(%)	7.8i	1.0i	0.0i	0.4i	2.8i
% change	(%)		-87.2	-100.0	-94.5	-64.7
Kentucky bluegrass						
Shoot frequency	(%)	59.5j	72.0j	21.3k	42.0j	37.3jk
% change	(%)		21.0	-64.2	-29.4	-37.3

Data from Manske 1992

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

Table 9. Shoot frequency of shrubs on the seasonal period of every-other-year burn treatments and percent change from nonburned control.

Plant Biotypes		No Burns 6 reps	Early Spring (mid-late Apr) 1 rep	Spring (May-mid Jun) 3 reps	Early Summer (mid Jun-Jul) 7 reps	Mid Summer (early-mid Aug) 4 reps
Western snowberry						
Shoot frequency	(%)	58.3a	5.0b	10.3b	33.4ab	21.5b
% change	(%)		-91.4	-82.3	-42.7	-63.1
Western rose						
Shoot frequency	(%)	35.8c	8.0d	4.3d	41.7c	41.3c
% change	(%)		-77.7	-87.9	16.4	15.1
Silverberry						
Shoot frequency	(%)	17.3e	2.0f	7.3e	6.6e	0.5f
% change	(%)		-88.5	-57.7	-62.1	-97.1

Data from Manske 1992

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

Table 10. Mycorrhizal fungal infection of plant roots and soil mineral nitrogen (NH_4-NO_3) on the number of repeated every-other-year burn treatments.

Plant Biotypes		No Burns 6 reps	One Burn 4 reps	Two Burns 4 reps	Three Burns 4 reps	Four Burns 3 reps
Western snowberry Fungi infection	(%)	93.8a	84.7a	84.3a	85.2a	85.9a
Smooth bromegrass Fungi infection	(%)	32.3b	55.0b	50.0b	31.4b	40.1b
Western wheatgrass Fungi infection	(%)	66.0c	67.0c	61.3c	76.8c	63.8c
Blue grama Fungi infection	(%)	78.8d	77.1d	84.9d	79.9d	73.5d
Mineral Nitrogen NH_4-NO_3	(ppm)	9.56e	9.65e	9.41e	5.54e	8.36e

Data from Manske 1992

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

Table 11. Mycorrhizal fungal infection of plant roots and soil mineral nitrogen (NH_4-NO_3) on the seasonal period of every-other-year burn treatments.

Plant Biotypes		No Burns 6 reps	Early Spring (mid-late Apr) 1 rep	Spring (May-mid Jun) 3 reps	Early Summer (mid Jun-Jul) 7 reps	Mid Summer (early-mid Aug) 4 reps
Western snowberry Fungi infection	(%)	93.8a	92.3a	85.5a	82.7a	86.6a
Smooth bromegrass Fungi infection	(%)	32.3b	33.7b	40.0b	37.2b	65.7b
Western wheatgrass Fungi infection	(%)	66.0c	74.7c	48.0c	73.7c	69.5c
Blue grama Fungi infection	(%)	78.8d	70.7d	79.6d	82.0d	76.2d
Mineral Nitrogen NH_4-NO_3	(ppm)	9.56e	3.64	8.47e	9.42e	7.09e

Data from Manske 1992

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

Fig. 1. Western snowberry colony before (left) and after (right) four every-other-year prescribed burns during mid summer (August). Photographs were taken by Karen Smith.

Literature Cited

Barker, W.T., and W.C. Whitman. 1988. Vegetation of the Northern Great Plains. Rangelands 10:266-272.

Bragg, T.B. 1995. The physical environment of North American grasslands. *in* K. Keeler and A. Joern (eds.). The changing prairie. Oxford University Press. New York, NY.

Coleman, C.D., C.P.P. Reid, and C.V. Cole. 1983. Biological strategies of nutrient cycling in soil ecosystems. Advances in Ecological Research 13:1-55.

Cook, C.W., and J. Stubbendieck. 1986. Range research: basic problems and techniques. Society for Range Management, Denver, CO. 317p.

Giovannetti, M., and B. Mosse. 1980. An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. New Phytol. 84:489-500.

Gorder, M.M., L.L. Manske, and T.L. Stroh. 2004. Grazing treatment effects on vegetative tillering and soil rhizospheres of western wheatgrass. NDSU Dickinson Research Extension Center. Range Research Report DREC 04-1056. Dickinson, ND. 13p.

Higgins, K.F. 1986. Interpretation and compendium of historical fire accounts in the Northern Great Plains. US Fish and Wildlife Service. Resource Publication 161. 39p.

Ingham, R.E., J.A. Trofymow, E.R. Ingham, and D.C. Coleman. 1985. Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. Ecological Monographs 55:119-140.

Keeney, D.R. 1982. Nitrogen - availability indices. p. 711-733. *in* R.H. Miller and D.R. Keeney (eds.). Methods of soil analysis. 2nd ed. American Society of Agronomy, Madison, WI.

Keeney, D.R., and D.W. Nelson. 1982. Nitrogen - inorganic forms. p. 643-698. *in* R.H. Miller and D.R. Keeney (eds.). Methods of soil analysis. 2nd ed. American Society of Agronomy, Madison, WI.

Kormanik, P.P., and A.C. McGraw. 1982. Quantification of vesicular arbuscular mycorrhizae in plant roots. p. 37-45. *in* N.C. Schenek (ed.). Methods and principles of mycorrhizal research. American Phytopathological Society, St. Paul, MN.

Manske, L.L., W.T. Barker, and M.E. Biondini. 1988. Effects of grazing management treatments on grassland plant communities and prairie grouse habitat. USDA Forest Service. General Technical Report RM-159. p. 58-72.

Manske, L.L. 1992. Effects from prescribed burning treatments repeated every other year on shrub invaded mixed grass prairie. Report to USDI Fish and Wildlife Service. Lostwood National Wildlife Refuge. Kenmare, ND.

Manske, L.L. 2005. Biological management of western snowberry. NDSU Dickinson Research Extension Center. Range Management Report DREC 05-1060. Dickinson, ND. 12p.

Mosteller, F., and R.E.K. Rourke. 1973. Sturdy Statistics. Addison-Wesley Publishing Co., Reading, MA. 395p.

Phillips, J.M., and D.S. Hayman. 1970. Improved procedures for clearing and straining parasitic and vesicular arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. Br. Mycol. Soc. 55:158-161.

Sarvis, J.T. 1941. Grazing investigations on the Northern Great Plains. North Dakota Agricultural Experiment Station. Bulletin 308. Fargo, ND.

Smith, K.A. 1985a. Prescribed burning reduces height and canopy cover of western snowberry (North Dakota). Restoration and Management Notes 3:86-87.

Smith, K.A. 1985b. Canada thistle response to prescribed burning (North Dakota). Restoration and Management Notes 3:87.

Smith, K.A. 1988. Lostwood National Wildlife Refuge station plan. US Fish and Wildlife Service.

Smith, K.A. 1997. Lostwood National Wildlife Refuge comprehensive management plan. US Fish and Wildlife Service.

Wright, H.A., and A.W. Bailey. 1982. Fire ecology. John Wiley and Sons. New York, NY.

Grazing and Burning Treatment Effects on Soil Mineral Nitrogen and Rhizosphere Volume

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Insufficient nitrogen availability limits productivity more often than water in temperate grasslands (Tilman 1990). Enhancement of the nitrogen cycle in grassland ecosystems that causes an increase in available inorganic (mineral) nitrogen results in greater productivity of herbage, livestock, and wildlife.

Soil organic matter of mixed grass prairie ecosystems generally contains about three to eight tons of organic nitrogen per acre. Organic nitrogen is a form of nitrogen not directly usable by grass plants. Organic nitrogen must be converted into mineral nitrogen in order to be usable by plants. The biogeochemical processes of the nitrogen cycle in grassland ecosystems that convert nitrogen into the various forms are a function of the interactions among rhizosphere organisms, grass plants, and large grazing herbivores (Manske 1999).

This project uses soil mineral nitrogen and rhizosphere volume data to evaluate the effects that grazing treatments and burning treatments have on rhizosphere organism activity and on enhancement of biogeochemical processes of the nitrogen cycle in grassland ecosystems and the resulting increase in quantity of available mineral nitrogen converted from soil organic nitrogen.

Study Areas

This project was conducted at two locations. The NDSU Dickinson Research Extension Center ranch is located in Dunn county in western North Dakota, at 47° 14' north latitude, 102° 50' west longitude. Mean annual temperature is 42.5° F (5.8° C). January is the coldest month, with a mean temperature of 14.5° F (-9.7° C). July and August are the warmest months, with mean temperatures of 69.4° F (20.8° C) and 68.8° F (20.4° C), respectively. Long-term (1982-2006) mean annual precipitation is 16.87 inches (428.59 mm). The growing-season precipitation (April through October) is 14.09 inches (357.86 mm) and is 83.50% of the annual precipitation. June has the greatest monthly precipitation, at 3.27 inches (83.09 mm). The precipitation received during the 3-month period of May, June, and July (8.11 inches, 205.99 mm) accounts for 48.07% of the annual precipitation (Manske 2007a). Soils are primarily Typic Haploborolls developed on sedimentary deposits. The fine loamy soils have 5 to 6 tons of organic nitrogen per acre. Native vegetation is the Wheatgrass-Needlegrass Type (Barker and Whitman 1988) of the mixed grass prairie.

The USDI Lostwood National Wildlife Refuge is located in Burke and Mountrail counties in northwestern North Dakota between 48° 50' and 48° 30' north latitude and 102° 40' and 102° 20' west longitude. The region has cold winters and hot summers typical of continental climates. January is the coldest month, and July and August are the warmest months. Long-term (1936-1989) mean annual precipitation is 16.50 inches (419.10 mm). The growing-season precipitation (April through October) is 13.80 inches (350.52 mm) and is 83.64% of the annual precipitation. June has the greatest monthly precipitation, at 3.32 inches (84.33 mm). The precipitation received during the 3-month period of May, June, and July (7.70 inches, 195.58 mm) accounts for 46.67% of the annual precipitation (Manske 2007b). Soils are primarily Typic Haploborolls and Typic Argiborolls developed on glacial terminal moraine. The fine loamy soils have 4 to 6 tons of organic nitrogen per acre. Native vegetation is the Wheatgrass-Needlegrass Type (Barker and Whitman 1988) of the mixed grass prairie.

Procedures

The effects from defoliation treatments on enhancement of the nitrogen cycle and rhizosphere organism biomass and activity were evaluated from differences in soil mineral nitrogen content and in rhizosphere volume. The quantitative soil mineral nitrogen study was conducted on grazing treatments and on repeated prescribed burning treatments. The quantitative rhizosphere volume study was conducted on grazing treatments.

The grazing treatments were conducted at the Dickinson Research Extension Center ranch between 1983 and 2002 on mixed grass prairie that had a history of management with moderate to heavy seasonlong grazing. The treatments were (1) long-term nongrazed control (NG), (2) 6.0-month seasonlong (6.0-m SL), (3) 4.5-month seasonlong (4.5-m SL), and (4) twice-over rotation (TOR). Each of the grazing treatments had two replications. The long-term nongrazed management treatment had not been grazed, mowed, or burned for more than 30 years before the initiation of these research treatments in 1983. Livestock on the 6.0-month seasonlong management treatment grazed one native range pasture for 6.0 months (183 days) from mid May until mid November. Livestock on the 4.5-month seasonlong management treatment grazed one native range pasture for 4.5 months (135 days) from early June until mid October. Livestock on the twice-over rotation management treatment followed a double rotation sequence through three native range pastures for 4.5 months (135 days) from early June until mid October. Each of the three pastures in the rotation were grazed for about 15 days during the first period, the 45-day interval from 1 June to 15 July. During the second period, after mid July and before mid October, each pasture was grazed for double the number of days it was grazed during the first period.

The repeated every-other-year prescribed burning treatments were conducted by refuge manager Karen Smith at the Lostwood National Wildlife Refuge during a thirteen year period between 1978 and 1990 on degraded mix grass prairie that had greater than 50% of the upland occupied with western snowberry colonies (Smith 1988). The number of repeated every-other-year prescribed burns was (1) no burns control, (2) one burn, (3) two burns, (4) three burns, and (5) four burns. The prescribed burns were conducted during four seasons: (6) early spring, (7) spring, (8) early summer, and (9) mid summer. Annual burns were not possible because of insufficient production of plant biomass for fuel (Smith 1985). The refuge land had not been burned for more than 100 years before the initiation of these prescribed burn treatments in 1978. However, between 1940 and 1975, about 26% of the refuge was annually grazed with a deferred-type seasonlong management for 4.5 to 5.0 months at low to moderate stocking rates, primarily during July through November (Smith 1988). Some areas were grazed only one time and other areas were grazed as many as 22 times over the 35-year period (Smith 1988). About 15% of the refuge was never burned, grazed, or mowed (Smith 1997). The no burns control treatment had 6 replications with an average size of 436.8 acres (176.90 ha) and had no grazing, mowing, or burning during the thirteen year study period. The every-other-year prescribed burning treatments had an average size of 530.5 acres (214.85 ha) and had no grazing or mowing during the thirteen year study period. The one burn, two burns, and three burns treatments had 4 replications each, and the four burns treatment had 3 replications. The early spring burns had 1 replication, the spring burns had 3 replications, the early summer burns had 7 replications, and the mid summer burns had 4 replications.

The quantitative soil mineral nitrogen study was conducted on the nongrazed, 4.5-month seasonlong, and twice-over rotation grazing treatments; on the no burns, one burn, two burns, three burns, and four burns every-other-year prescribed burning treatments; and on the early spring, spring, early summer, and mid summer every-other-year prescribed burning treatments. Field samples of grazing and burning treatment soils were collected from nearly level loam soils. Aboveground vegetation was clipped from soil sample areas and discarded. Each soil field sample consisted of five soil cores that were air dried, ground, and thoroughly mixed. Twenty percent of each field sample was retained for quantitative laboratory analysis.

Field samples were collected during mid June 1989 at the start of the seventh year of the grazing treatment study. Each soil core from the grazing treatments was collected with a bucket auger and was 2 inches (5.08 cm) in diameter and 6 inches (15.24 cm) in depth. Two field samples were collected in each of the two replications of each nongrazed control and grazing treatment, resulting in four replicated field samples per grazing treatment.

Field samples were collected during July and August 1990 after thirteen years of every-other-year prescribed burning treatments. Each soil core from the burn treatments was collected with a soil probe and was 1 inch (2.54 cm) in diameter and 6 inches (15.24 cm) in depth. One field sample was collected during each time period for each replication of the no burns and the seasonal period and number of repeated every-other-year prescribed burning treatments. A mean of the July and August sample periods was determined for each treatment replication.

In the laboratory, subsamples of soil from the field samples were analyzed for total incubated mineralizable nitrogen (N) using procedures outlined by Keeney (1982). Inorganic forms of nitrogen were extracted from the soil subsamples by adding a reagent; alkaline phosphate-borate buffer to the grazing treatment soils, and 2 M KCl to the burning treatment soils. The mixtures of reagent and soil were shaken for one hour. The extract was quantified into parts per million (ppm) of mineral nitrogen, ammonia (NH_3), ammonium (NH_4), and nitrate NO_3), with steam distillation (Keeney and Nelson 1982). These quantified values of mineral nitrogen were converted from parts per million to pounds per acre-foot. Soil nitrite (NO_2) was not quantified because it is seldom present in detectable amounts.

The rhizosphere volume study was conducted on the nongrazed (NG), 6.0-month seasonlong (6.0-m SL), 4.5-month seasonlong (4.5-m SL), and twice-over rotation (TOR) grazing treatments in 2002 during the twentieth year of the grazing treatment study. Two replications of soil cores containing western wheatgrass roots and rhizospheres were collected monthly during June, July, August, and September from nearly level loam soils in each grazing treatment. Plastic PVC pipe 3 inches (7.62 cm) in diameter and 4 inches (10.16 cm) long was forced into sample site soil. Intact soil-plant-rhizosphere cores and pipe were excavated and transported to the laboratory.

In the laboratory, the soil matrix of collected soil cores was carefully removed from between the rhizospheres surrounding the roots of western wheatgrass plants. The roots and rhizospheres of other plant species were separated from the soil cores and discarded. The western wheatgrass rhizospheres were sprayed with a clear acrylic coating to prevent damage during further handling. The length and diameter of the rhizosphere around each root of every plant, including associated tillers, were measured with a vernier caliper. During the process of extraction from matrix soil, portions of some rhizospheres were damaged and small segments were detached from the root surface. The length measurements of damaged rhizospheres were the length of the root, including the regions of detached rhizosphere segments. The length and diameter measurements were used to determine the volume of the rhizosphere around each root. The sum of the individual roots' rhizosphere volume was the total rhizosphere volume per replicated soil core. The total rhizosphere volume reported as cubic centimeters per cubic meter of soil (Gorder, Manske, and Stroh 2004) was converted to cubic feet per acre-foot. Differences among treatments in the means of mineral nitrogen content and rhizosphere volume were analyzed by a standard paired-plot t-test (Mosteller and Rourke 1973).

Results

Precipitation during the 1989 growing season at the Dickinson Research Extension Center ranch was low at 10.60 inches (75.24% of LTM). During 1989, plants experienced water stress during July, August, and September. The previous growing season of 1988 had drought conditions receiving only 5.30 inches of precipitation (37.62% of LTM). During 1988, plants experienced water stress during April, June, July, August, September, and October. The drought of 1988 started in August 1987 and near-drought conditions lasted through the growing season of 1992 (Manske 2007a).

Precipitation during the 1990 growing season at the Lostwood Wildlife Refuge was near normal at 14.44 inches (104.64% of LTM). Below normal precipitation occurred during June, September, and October. The previous growing season of 1989 had low precipitation at 10.84 inches (78.55% of LTM). Below normal precipitation occurred during April, May, August, and October. The growing season of 1988 had drought conditions receiving 9.61 inches (69.64% of LTM). Below normal precipitation occurred during April, July, August, and October (Manske 2007b).

Precipitation during the 2002 growing season at the Dickinson Research Extension Center ranch was greater than normal at 18.85 inches (133.79% of LTM). June, July, and August were wet months with precipitation greater than 125% of LTM. September and October had water deficiencies receiving precipitation at less than 75% of LTM and plants experienced water stress during September (Manske 2007a).

Mineral nitrogen in pounds per acre-foot (lbs/ac-ft) is the quantity of mineral nitrogen available in the soil and usable by grassland plants for growth of aboveground herbage and belowground root biomass. Differences in the pounds of available mineral nitrogen on the grazing treatments and burning treatments indicates the differences in the effects the defoliation treatments have on the rhizosphere organism activity and on the enhancement of the nitrogen cycle and the quantity of mineral nitrogen converted from soil organic nitrogen.

The mineral nitrogen available on the one, two, three, and four repeated every-other-year burning treatments and on the early spring, spring, early summer, and mid summer seasonal every-other-year burning treatments was low and was not significantly different ($P<0.05$) from that on the no burns control treatment (table 1). The number of repeated every-other-year burning treatments and the seasonal period of prescribed burning treatments did not affect the quantity of available mineral nitrogen in the soil. The mineral nitrogen available on all of the every-other-year burning treatments and no burns control treatment was significantly less ($P<0.05$) than the mineral nitrogen available on all of the grazing treatments and nongrazed control treatment (table 1, figure 1). The mineral nitrogen available on the no burns treatment and every-other-year prescribed burning treatments was less than 30% of the mineral nitrogen available on the nongrazed treatment. The antagonistic effects on the rhizosphere organism activity from the previous management with deferred grazing practices caused the available mineral nitrogen to decrease 70.6% on the no burns treatment and to decrease 74.5% on the prescribed repeated burning treatments.

The mineral nitrogen available on the 4.5-m and 6.0-m seasonlong grazing treatments and on the nongrazed control treatment were significantly different ($P<0.05$) (table 1, figure 1). After six grazing seasons, the seasonlong grazing treatments did not beneficially affect the rhizosphere organisms and the biogeochemical nitrogen cycle processes and did not increase the quantity of available mineral nitrogen. The seasonlong grazing treatments were antagonistic to rhizosphere organism activity causing a reduction in the quantity of soil organic nitrogen converted into mineral nitrogen.

The mineral nitrogen available on the twice-over rotation treatment was more than 100 lbs/ac and was significantly greater ($P<0.05$) than that on the 4.5-m and 6.0-m seasonlong grazing treatments and on the nongrazed control treatment (table 1, figure 1). The twice-over rotation treatment beneficially affected the rhizosphere organisms and the available mineral nitrogen was increased 67.7% greater than on the nongrazed treatment and 131.9% and 188.7% greater than on the seasonlong grazing treatments.

The twice-over rotation treatment consisted of three native range pastures grazed for about 15 days each during the first period from 1 June to 15 July when grass tillers are between the three and a half new leaf stage and the flowering stage. The available mineral nitrogen was high on each of the three rotation pastures and was not significantly different ($P<0.05$) among the first, second, and third pasture grazed in the rotation sequence (table 2). Effects from first period grazing treatments on the first, second, and third pastures of the twice-over rotation sequence stimulated the rhizosphere organism activity that increased the mineral nitrogen 87.7%, 54.6%, and 60.8% greater than that on the nongrazed treatment, respectively.

Rhizosphere volume in cubic feet per acre-foot ($ft^3/ac\text{-}ft$) is the quantity of space occupied by active rhizosphere organisms on the grazing treatments. Differences in rhizosphere volume indicates the differences in the effects the grazing treatments have on the rhizosphere organism biomass and activity and subsequently on the proportional differences in the quantity of mineral nitrogen converted from soil organic nitrogen.

Rhizosphere volume on the 6.0-m seasonlong grazing treatment was significantly lower ($P<0.05$) than that on the nongrazed control treatment (table 1, figure 2) and was lower than, but not significantly different ($P<0.05$) from, that on the 4.5-m seasonlong grazing treatment (table 1, figure 2). The rhizosphere volume was greatly reduced in size as a result of the antagonistic effects from the 6.0-m seasonlong treatment on rhizosphere organism activity. The rhizosphere volume on the 6.0-m seasonlong treatment was 51.2% smaller than on the nongrazed treatment and 26.4% smaller than on the 4.5-m seasonlong treatment. Rhizosphere volume on the 4.5-m seasonlong grazing treatment was lower than, but not significantly different ($P<0.05$) from, that on the nongrazed control treatment (table 1, figure 2). After 20 grazing seasons, the 4.5-m seasonlong treatment was slightly antagonistic to the activity of the rhizosphere organisms. The rhizosphere volume was 33.7% smaller on the 4.5-m seasonlong treatment than on the nongrazed treatment. Rhizosphere volume on the twice-over rotation treatment was significantly greater ($P<0.05$) than the rhizosphere volume on the 6.0-m seasonlong and the 4.5-m seasonlong grazing treatments and on the nongrazed control treatment (table 1, figure 2). The twice-over rotation treatment greatly stimulated the activity of the rhizosphere organisms. The rhizosphere volume on the twice-over rotation treatment was 356.4%, 235.8%, and 122.7% greater than on the 6.0-m seasonlong, 4.5-m seasonlong, and nongrazed treatments, respectively.

Rhizosphere volume changes as a result of increases or decreases in rhizosphere organism activity. The effects on rhizosphere volume during the growing season from the grazing treatments are shown in figures 3 and 4. Rhizosphere volume on the nongrazed control treatment increased slightly during the early summer in July and remained at about the same volume for the duration of the season. The volume at the end of the season on the nongrazed treatment was about 40% greater than the volume at the beginning. Rhizosphere volume on the 6.0-m seasonlong grazing treatment declined gradually during the growing season and the volume at the end of the season was less than half the volume of the beginning. The 6.0-m seasonlong treatment was antagonistic to the activity of the rhizosphere organisms during the entire grazing period. The rhizosphere volume on the 6.0-m seasonlong treatment was significantly reduced ($P<0.05$) and was 73% less than that on the nongrazed treatment. Rhizosphere volume on the 4.5-m seasonlong treatment remained about the same during the growing season except for a substantial decrease during July. The volume at the end of the season was the same as the volume at the beginning. The antagonistic effects on rhizosphere organism activity from the 4.5-m seasonlong treatment caused a 35.2% decrease in rhizosphere volume, but not significant ($P<0.05$) from that on the nongrazed treatment. Rhizosphere volume on the twice-over rotation treatment increased slowly during the early growing season and then, following the first grazing period that occurred when grass tillers were between the three and a half new leaf stage and the flower stage from early June to mid July, the volume increased rapidly and more than doubled in size. At the end of the growing season, the volume on the twice-over rotation treatment was 105% greater than the volume at the beginning. The twice-over rotation treatment greatly stimulated the activity of the rhizosphere organisms. The rhizosphere volume on the twice-over rotation treatment significantly increased ($P<0.05$) and was 900.6%, 265.3%, and 170.1% greater than the rhizosphere volumes on the 6.0-m seasonlong, 4.5-m seasonlong, and nongrazed treatments, respectively.

The first grazing period on the third pasture in the twice-over rotation sequence was for 15 days during early July. The rhizosphere volume increased 20.3% during the two weeks following the first grazing period and increased 85.7% during the next five weeks (figure 5). The rhizosphere volume increased 123.4% in size because of the enhanced rhizosphere organism activity that resulted from the beneficial effects of partial defoliation during the first grazing period on the twice-over rotation treatment.

Discussion

In grassland ecosystems, the conversion of plant usable mineral nitrogen from soil organic nitrogen requires active rhizosphere organisms. Rhizosphere organisms require short chain carbon exudates from roots of grass plants. Rhizosphere organisms trade nitrogen to grass plants for carbon, and grass plants trade carbon to soil microorganisms for nitrogen. This interdependent symbiotic relationship between grass plants and rhizosphere organisms is controlled by partial defoliation of aboveground plant parts. The effects of defoliation can be beneficial or antagonistic depending on the degree of foliage removal and phenological growth stage of the grass tillers. Knowledge of grass developmental morphology and physiological processes that help grass tillers withstand and recover from defoliation is necessary to comprehend the biological requirements of grasses and the effects from defoliation management practices.

Grazing Defoliation

Grass plants have developed defoliation resistance mechanisms in response to grazing during the period of coevolution with herbivores (McNaughton 1979, 1983; Coleman et al. 1983; Briske and Richards 1995; Manske 1999) that help grass tillers withstand and recover from partial defoliation by grazing.

Traditional grazing management practices are not beneficial for grassland ecosystems. The deferred grazing, 6.0-m seasonlong, and 4.5-m seasonlong management strategies are antagonistic to rhizosphere organism activity and biogeochemical processes of the nitrogen cycle and these traditional grazing practices do not stimulate beneficial grass growth processes. The rhizosphere organism biomass and activity and the quantity of available mineral nitrogen decrease by small amounts annually along with proportional decreases in grass density and herbage biomass production. After two, three, or more decades of management of grassland ecosystems with traditional grazing practices, the losses in productivity are substantial. The deferred grazing strategy caused a 70.6% decrease in available mineral nitrogen after 35 years of treatment. The 6.0-m seasonlong grazing strategy caused a 41.9% decrease in mineral nitrogen and a 51.2% decrease in rhizosphere volume after 20 years of seasonlong treatment. The 4.5-m seasonlong grazing strategy caused a 27.7% decrease in mineral nitrogen after 6 years of treatment and caused a 33.7% decrease in rhizosphere volume after 20 years of treatment.

The twice-over rotation grazing management strategy is beneficial for grassland ecosystems. The advantageous effects from partial defoliation managed with a twice-over rotation grazing strategy caused a 67.7% increase in available mineral nitrogen after six years of treatment and caused a 122.7% increase in rhizosphere volume after 20 years of treatment.

Burning Defoliation

Prescribed burning of grasslands severely removes all or nearly all of the aboveground plant material. Complete defoliation by fire of grass tillers does not activate the defoliation resistance mechanisms that help grass tillers withstand and recover from partial defoliation. Replacement of fire removed plant material must develop from crown buds and stored root carbohydrate reserves. Growth of roots and shoots that depends on stored carbohydrates occurs at greatly reduced rates (Coyne et al. 1995) compared to replacement growth after partial defoliation by grazing that triggers the compensatory physiological processes, stimulates vegetative reproduction by tillering, and stimulates rhizosphere organism activity with the resulting increase in available mineral nitrogen (Manske 1999).

The quantity of mineral nitrogen on the prescribed burning treatments and no burns treatment was not different, and was less than 30% of the quantity of mineral nitrogen on the nongrazed treatment, indicating that the previous management practices on the burning and no burns treatments were antagonistic to the rhizosphere organisms and the nitrogen cycle biogeochemical processes, and that none of the prescribed burning treatments stimulated activity of the rhizosphere organisms. The nongrazed treatment had more than 37 years with no defoliation events and had 106 pounds per acre-foot of available mineral nitrogen. The burning and no burns treatments had no grazing defoliation events during the period from 1975 to 1990, however, the entire area, except for about 15% of the land, was managed with periodic deferred-type seasonlong grazing from July through November in combination with full growing season rest for 35 years, between 1940 and 1975. As a result, the burning and no burns treatments had only around 31 pounds per acre-foot of available mineral nitrogen.

The intended purpose for deferment of grazing on a wildlife refuge was the avoidance of disturbance from grazing livestock of ground nesting birds from nest initiation through egg hatch. The intended biological purpose of deferred grazing was to increase grass density by promoting seedling development from increased seed stalk quantities and to use trampling by livestock to scatter and plant the resulting seeds. However, grassland ecosystem processes do not function in accordance with these proposed deferred grazing hypotheses.

The combination of periodic deferred-type seasonlong grazing and full growing season rest used to manage the Lostwood Wildlife Refuge between 1940 and 1975 caused the mixed grass prairie ecosystem to degrade and permitted the increase of western snowberry. This deterioration did not occur at a uniform rate. In the mid to late 1930's, only about 5% of the land area was occupied with western snowberry. The shrub composition in the plant community did not change much during the next 20 years. A substantial increase in shrub cover occurred between 1953 and 1969, and the western snowberry colonies expanded rapidly and infested extensive areas of degraded grassland between 1969 and 1975; as a result, over 50% of the upland was transformed into a shrubland of western snowberry and associated Kentucky bluegrass by 1979 (Smith 1988).

A prescribed repeated every-other-year burning regime designed with the intent to reduce the invading western snowberry and exotic grasses and to renovate the mixed grass prairie plant community (Smith 1985) was conducted for 13 years between 1978 and 1990. Nevertheless, the nitrogen cycle biogeochemical processes of the degraded grassland were not restored and the available mineral nitrogen was not increased by any of the prescibed burning treatments and, consequently, the quantity of aboveground biomass production on the burning treatments remained low and was not different from that produced on the no burns treatment (Manske 2007b). However, the percent composition of the aboveground biomass did change as a result of the prescribed burn treatments. The composition of introduced grasses, early succession and weedy forbs, and shrubs decreased with the increasing number of repeated prescribed burning treatments. Native grasses, sedges, and perennial forbs benefitted from the reduction in competition for sunlight from the decreased canopy cover of the taller shrubs (Manske 2007b).

Repeated prescribed burning does reduce undesirable opportunistic grasses, forbs, and shrubs. However, prescribed burning does not stimulate vegetative reproduction by tillering, prescribed burning does not stimulate endomycorrhizal fungal colonization of grass roots, prescribed burning does not stimulate rhizosphere organism biomass and activity, and prescribed burning does not stimulate conversion of soil organic nitrogen into mineral nitrogen (Manske 2007b).

Degraded grassland ecosystems are not restored by prescribed burning practices because restoration of native plant composition and biomass production takes place after the improvement of rhizosphere organism activity and the increase of available mineral nitrogen. Prescribed burning does not enhance the nitrogen cycle biogeochemical processes in grassland ecosystems.

Conclusion

Productivity on grassland ecosystems depends on the level of rhizosphere organism activity, on the quantity of available mineral nitrogen converted from soil organic nitrogen, and on the effectiveness of beneficial physiological processes within grass tillers.

Traditional grazing practices of deferred grazing, 6.0-m seasonlong, and 4.5-m seasonlong management are antagonistic to grass tiller biological requirements, and to rhizosphere organism biomass and activity. Over numerous growing seasons, the antagonistic effects from traditional grazing management result in greatly reduced biogeochemical processes of the nitrogen cycle and substantially decreased quantities of available mineral nitrogen that cause degradation of ecosystem plant communities and reduction of herbage biomass production. Nondefoliation management is antagonistic to grass tiller biological requirements and to rhizosphere organism biomass and activity causing slow degradation of the grassland ecosystem. The degree of ecosystem deterioration caused by the antagonistic effects from long-term nondefoliation treatments is greater than that from long-term traditional grazing management.

Fire has been an environmental factor on grassland ecosystems historically. Repeated prescribed burning reduces the undesirable opportunistic plants of introduced grasses, early succession and weedy forbs, and shrubs that increase in composition on degraded grassland ecosystems. However, prescribed burning that completely defoliates the plant material on grassland ecosystems does not stimulate beneficial physiological processes, does not stimulate rhizosphere organism biomass and activity, and does not stimulate conversion of mineral nitrogen from soil organic nitrogen. Consequently, the poor native plant species composition and the low herbage biomass production on degraded grassland ecosystems is not improved by burning. Repeated prescribed burning treatments do not restore degraded grassland ecosystems.

Partial defoliation controlled with the twice-over rotation grazing management strategy that removes 25% to 33% of the leaf material from grass tillers at phenological growth between the three and a half new leaf stage and the flower (anthesis) stage (early June to mid July); stimulates compensatory physiological processes resulting in greater replacement leaf, shoot, and root growth; stimulates vegetative reproduction by tillering resulting in greater grass tiller density and herbage biomass production; and stimulates rhizosphere organism biomass and activity resulting in quantities of available mineral nitrogen greater than 100 pounds per acre. Restoration of degraded grassland ecosystems and maintenance of healthy functioning grassland ecosystems requires annual partial defoliation by grazing that meets the biological requirements of grass tillers, that enhances rhizosphere organism activity, and that increases the quantity of available mineral nitrogen.

Grassland ecosystems have been customarily managed from the perspective of the “use”, e.g. for wildlife habitat or for livestock forage. The designated use receives priority consideration when management decisions are made. These management practices that focus on the use of a grassland ecosystem are antagonistic to the plants and to the rhizosphere organisms and cause reductions in grassland ecosystem productivity.

Management of partial defoliation by grazing that focuses on meeting the biological requirements of the plants and of the rhizosphere organisms is beneficial, and enhances the health and productivity of grassland ecosystems. Placing the decision priorities with the living components of the ecosystem is biologically effective, and results in greater forage for livestock, better habitat for wildlife, and more aesthetic open spaces for recreation and sightseeing as sustainable products from biologically managed grassland ecosystems.

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Table 1. Mineral nitrogen (lbs/acre-foot) for grazing treatments and repeated every-other-year burning treatments and rhizosphere volume (ft^3/acre-foot) for grazing treatments.

	Mineral (inorganic) Nitrogen lbs/acre-foot	Rhizosphere Volume ft^3/acre-foot
Grazing Treatments		
Nongrazed (NG)	106.05 b	101.93 y
6.0-m Seasonlong (6.0-m SL)	61.61 c	49.75 z
4.5-m Seasonlong (4.5-m SL)	76.70 c	67.61 yz
Twice-over Rotation (TOR)	177.84 a	227.06 x
Burning Treatments		
No Burns	31.20 d	
One Burn	31.49 d	
Two Burns	30.71 d	
Three Burns	18.08 d	
Four Burns	27.28 d	
Early Spring Burns	11.88	
Spring Burns	27.64 d	
Early Summer Burns	30.74 d	
Mid Summer Burns	23.14 d	

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

Table 2. Mineral nitrogen (lbs/acre-foot) for the three pastures of the twice-over rotation treatment.

	Mineral (inorganic) Nitrogen lbs/acre-foot
Twice-over Rotation (TOR)	
First pasture grazed	199.05 a
Second pasture grazed	163.97 a
Third pasture grazed	170.50 a
Three pasture mean	177.84 a

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

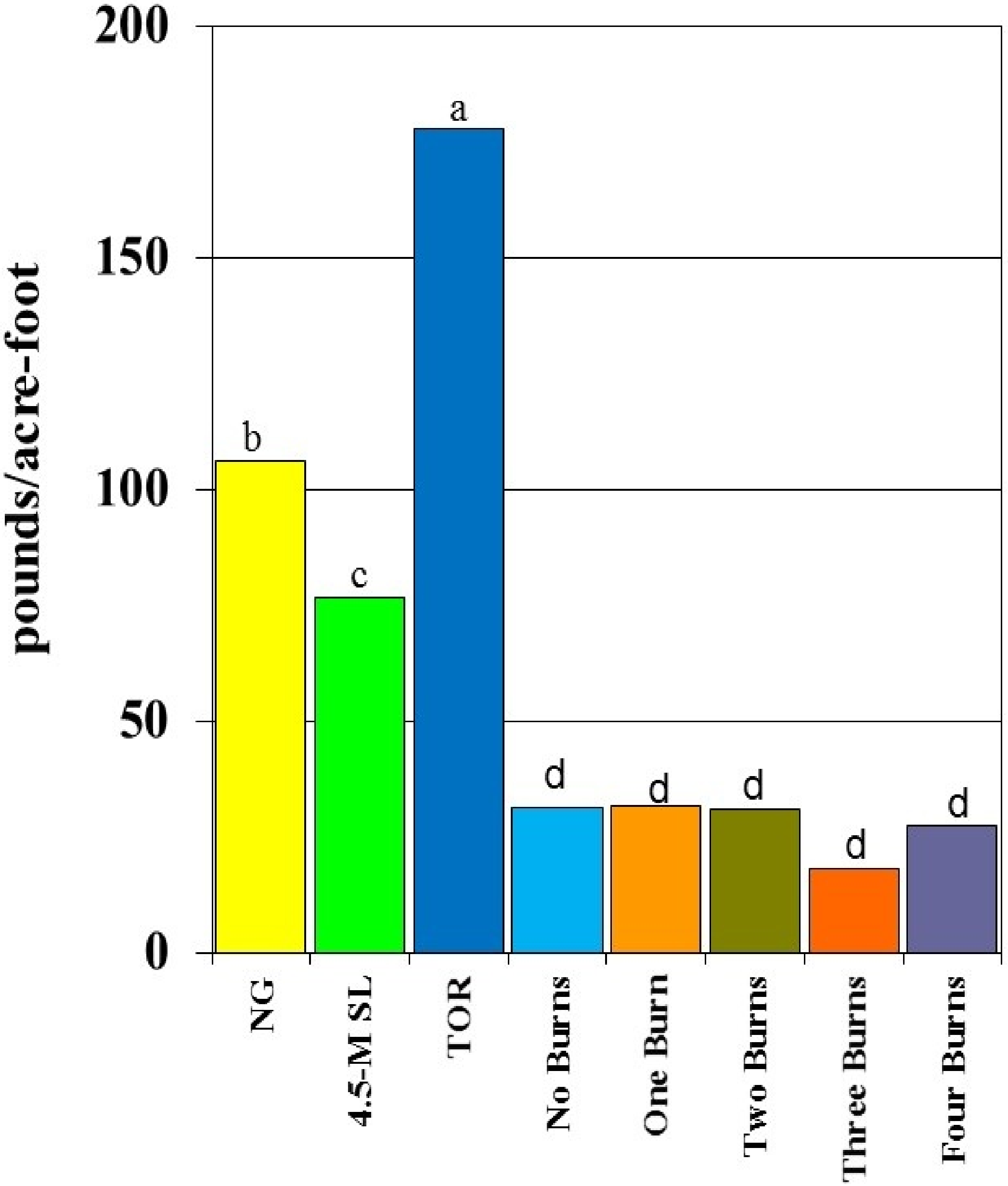

Figure 1. Mineral nitrogen in pounds per acre-foot for grazing treatments and every-other-year burn treatments.

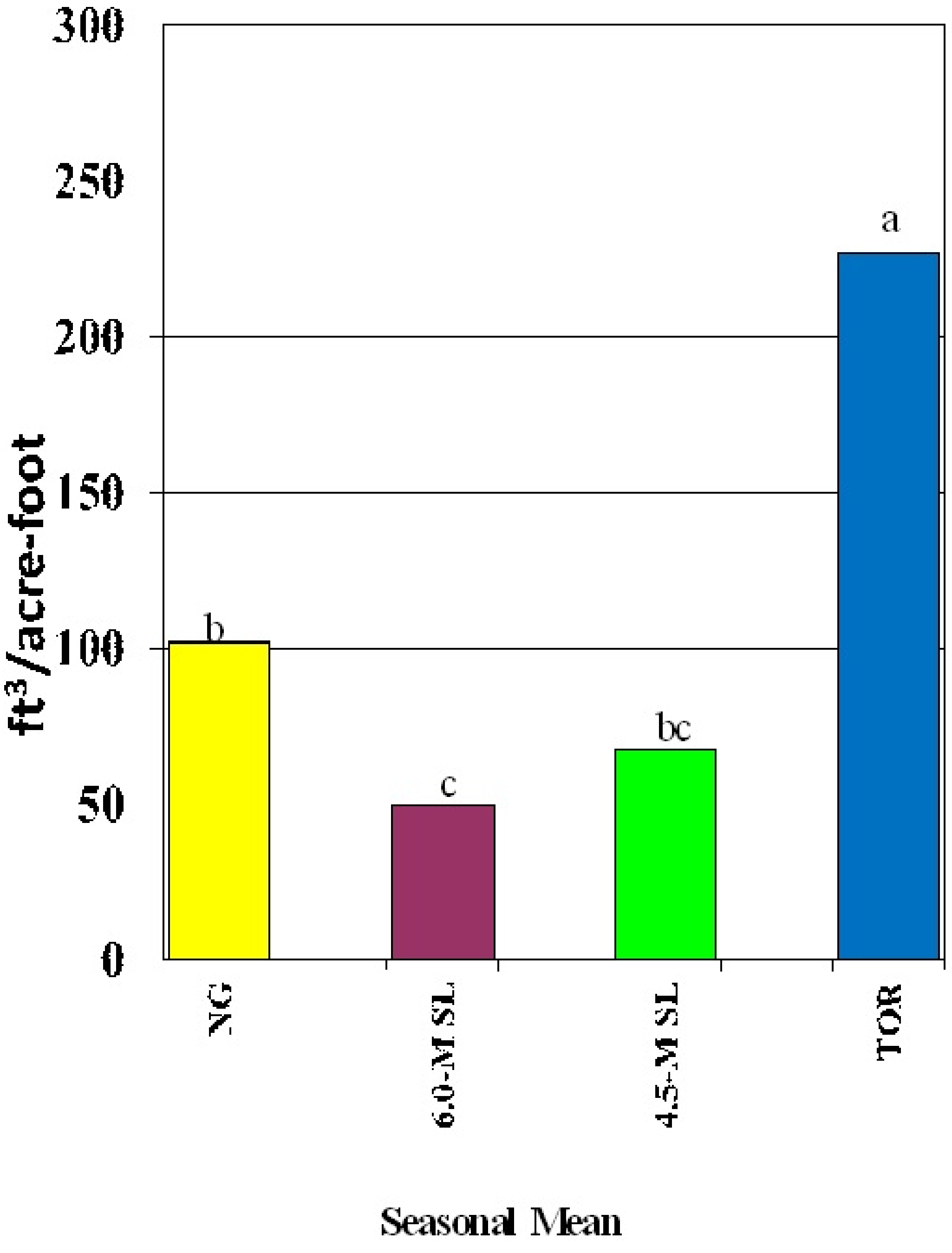

Figure 2. Seasonal mean rhizosphere volume in cubic feet per acre-foot for grazing treatments.

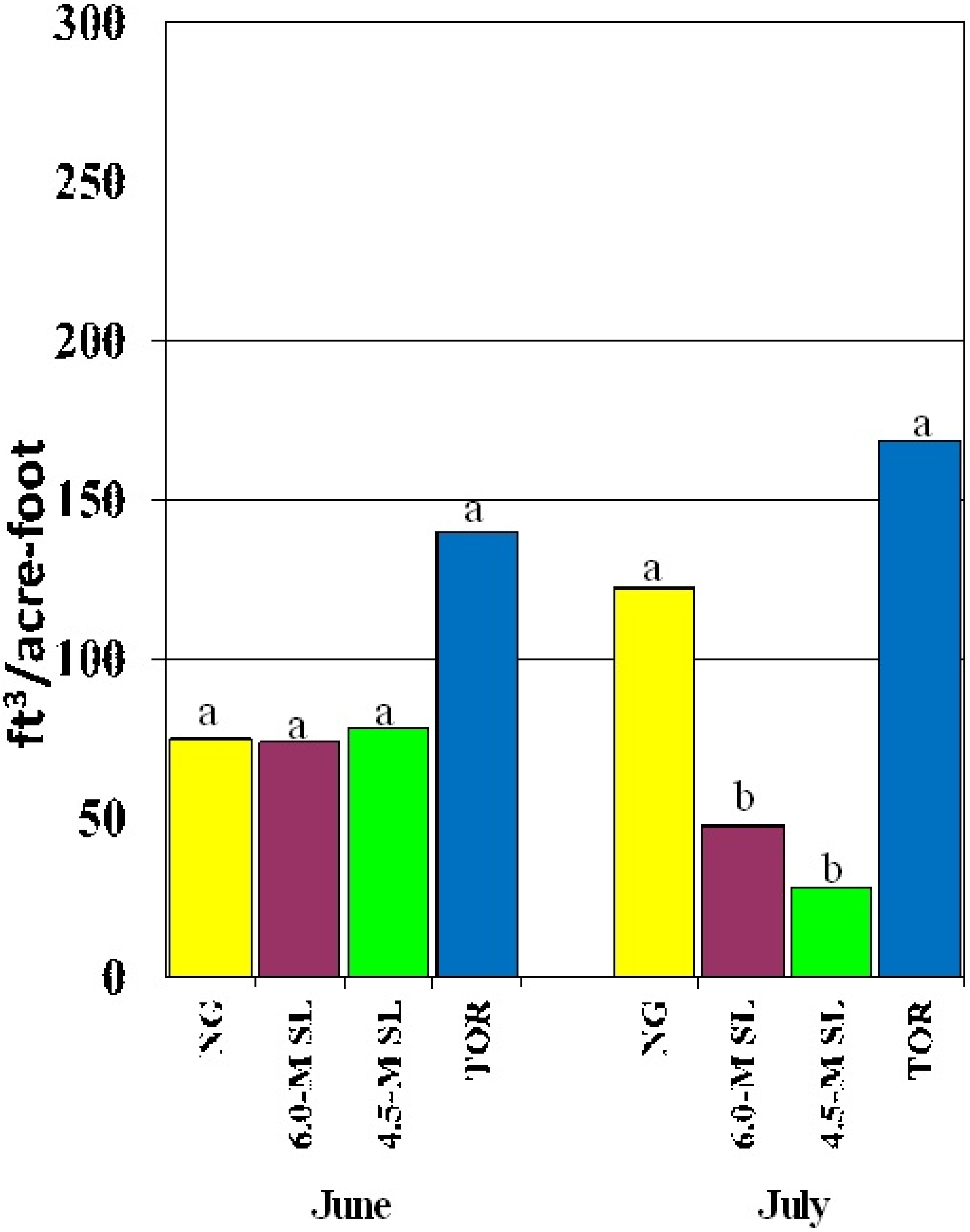

Figure 3. Monthly rhizosphere volume in cubic feet per acre-foot during June and July for grazing treatments.

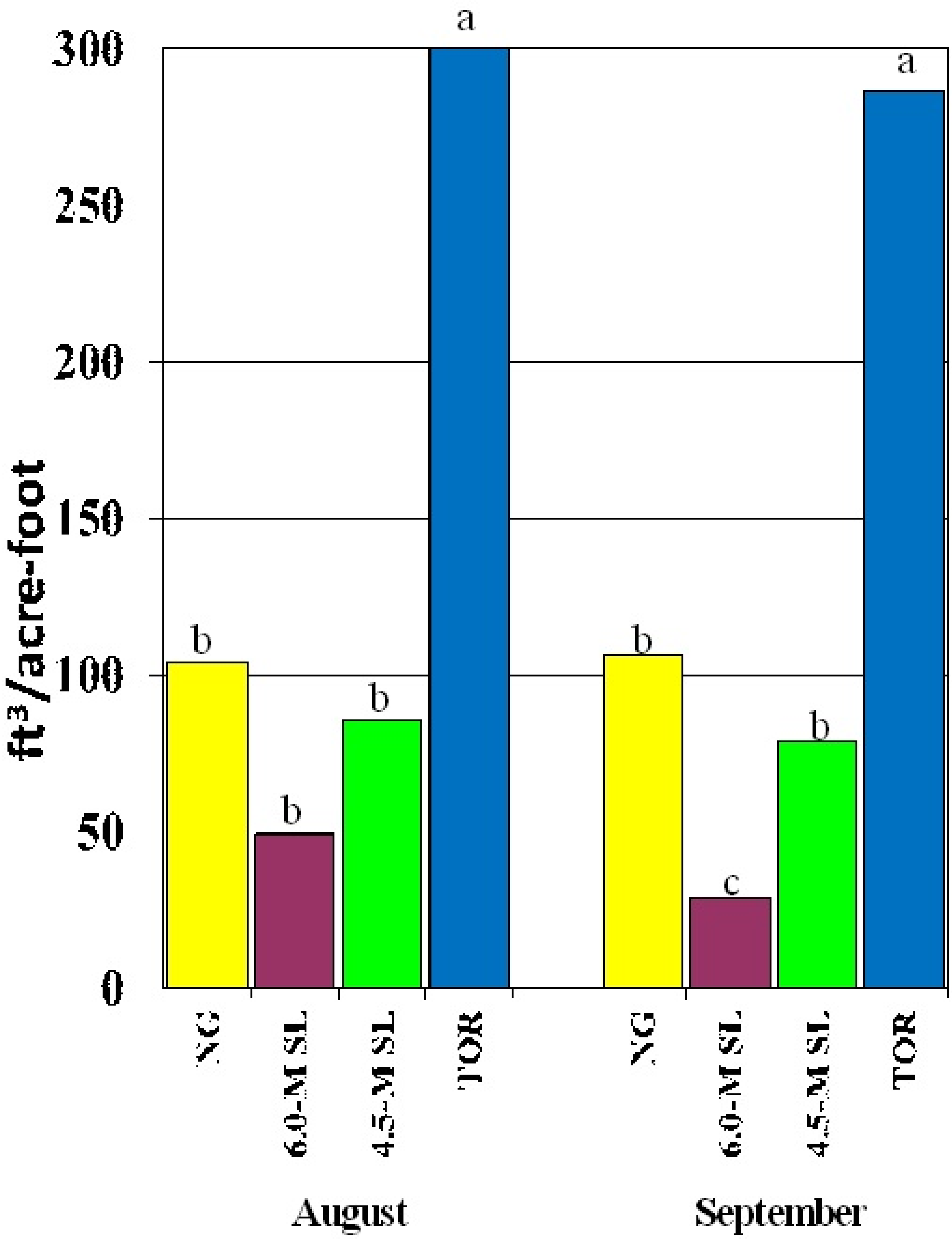

Figure 4. Monthly rhizosphere volume in cubic feet per acre-foot during August and September for grazing treatments.

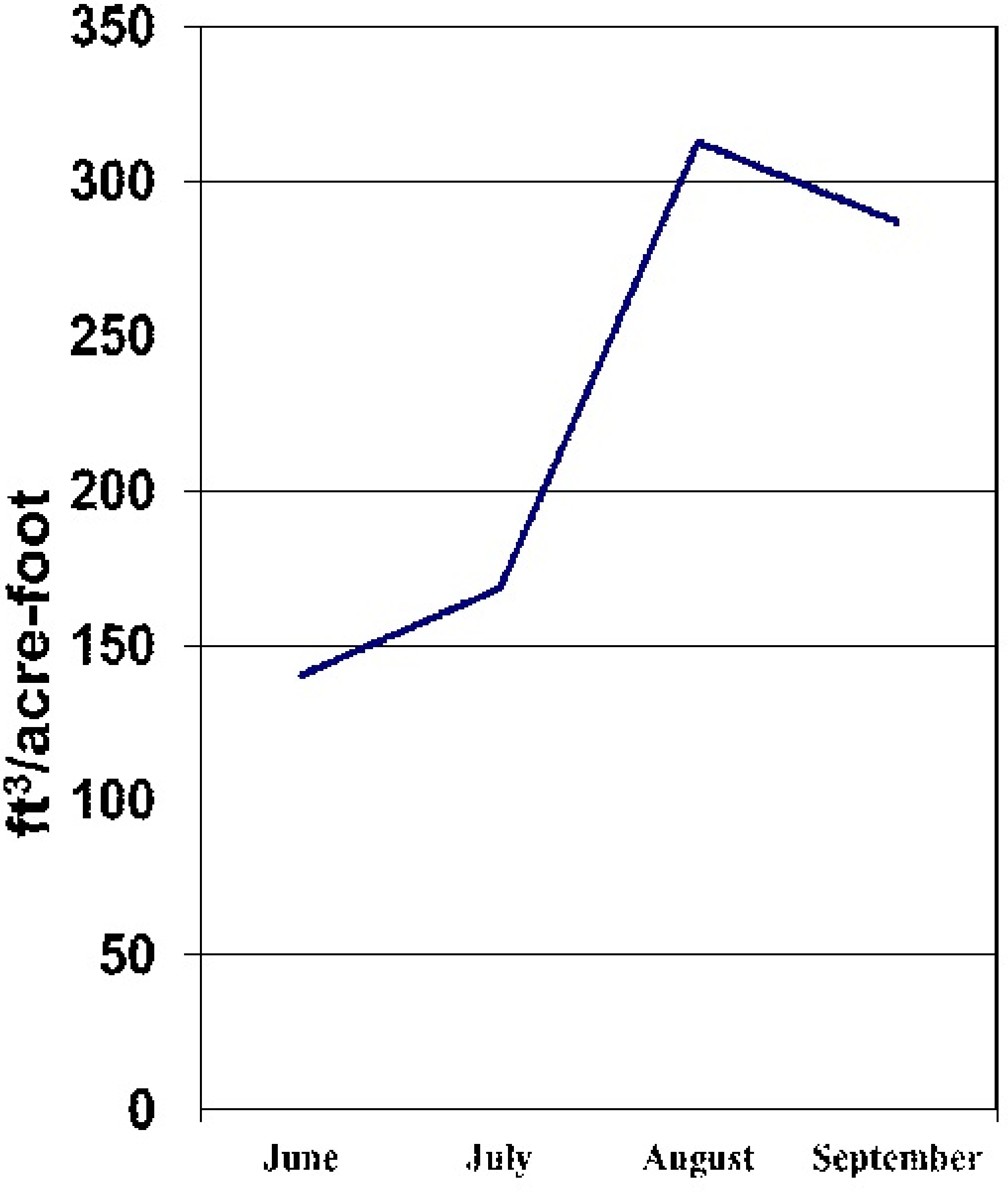

Figure 5. Rhizosphere volume change on the twice-over rotation treatment third pasture that was grazed for 15 days during early July.

Literature Cited

Barker, W.T., and W.C. Whitman. 1988. Vegetation of the Northern Great Plains. Rangelands 10:266-272.

Briske, D.D., and J.H. Richards. 1995. Plant response to defoliation: a physological, morphological, and demographic evaluation. p. 635-710. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Coleman, D.C., C.P.P. Reid, and C.V. Cole. 1983. Biological strategies of nutrient cycling in soil ecosystems. Advances in Ecological Research 13:1-55.

Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995. Carbon and nitrogen dynamics in range plants. p. 59-167. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Gorder, M.M., L.L. Manske, and T.L. Stroh. 2004. Grazing treatment effects on vegetative tillering and soil rhizospheres of western wheatgrass. NDSU Dickinson Research Extension Center. Range Research Report DREC 04-1056. Dickinson, ND. 13p.

Keeney, D.R. 1982. Nitrogen - availability indices. p. 711-733. *in* R.H. Miller and D.R. Keeney (eds.). Methods of soil analysis. 2nd ed. American Society of Agronomy, Madison, WI.

Keeney, D.R., and D.W. Nelson. 1982. Nitrogen - inorganic forms. p. 643-698. *in* R.H. Miller and D.R. Keeney (eds.). Methods of soil analysis. 2nd ed. American Society of Agronomy, Madison, WI.

Manske, L.L. 1999. Can native prairie be sustained under livestock grazing? p. 99-108. *in* J. Thorpe, T.A. Steeves, and M. Gollop (eds.). Proceedings of the Fifth Prairie Conservation and Endangered Species Conference. Provincial Museum of Alberta. Natural History Occasional Paper No. 24. Edmonton, Alberta, Canada.

Manske, L.L. 2007a. Ombrothermic interpretation of range plant water deficiency from temperature and precipitation data collected at the Ranch Headquarters of the Dickinson Research Extension Center in western North Dakota, 1982-2006. NDSU Dickinson Research Extension Center. Range Research Report DREC 07-1019j. Dickinson, ND. 17p.

Manske, L.L. 2007b. Effects on vegetation, endomycorrhizal fungi, and soil mineral nitrogen from prescribed burning treatments repeated every-other-year in mixed grass prairie invaded by western snowberry. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 07-3044. Dickinson, ND. 19p.

McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist 113:691-703.

McNaughton, S.J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329-336.

Mosteller, F., and R.E.K. Rourke. 1973. Sturdy Statistics. Addison-Wesley Publishing Co., MA. 395p.

Smith, K.A. 1985. Prescribed burning reduces height and canopy cover of western snowberry (North Dakota). Restoration and Management Notes 3:86-87.

Smith, K.A. 1988. Lostwood National Wildlife Refuge station plan. US Fish and Wildlife Service.

Smith, K.A. 1997. Lostwood National Wildlife Refuge comprehensive management plan. US Fish and Wildlife Service.

Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58:3-15.

Restoration of Degraded Prairie Ecosystems

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All prairie ecosystems that are not functioning at potential biological levels are degraded by some degree. Degradation of prairie ecosystems is caused by management practices that are antagonistic to the defoliation resistance mechanisms in perennial grasses. Restoration of degraded prairie ecosystems requires that managers understand the defoliation resistance mechanisms within grass plants, the symbiotic rhizosphere organisms' relationship with ecosystem biogeochemical processes, and the activation of these processes with defoliation by grazing animals.

Grass plants and large grazing herbivores evolved together. During the coevolutionary period, grasses developed biological processes that help plants withstand and recover from defoliation by grazing (Manske 2000a, 2007). Collectively, these processes are the Defoliation Resistance Mechanisms (McNaughton 1979, 1983; Coleman et al. 1983; Briske 1991; Briske and Richards 1995; Manske 1999). These mechanisms are: compensatory physiological processes within grasses (McNaughton 1979, 1983; Briske 1991); vegetative reproduction of secondary tillers from axillary buds (Mueller and Richards 1986; Richards et al. 1988; Murphy and Briske 1992; Briske and Richards 1994, 1995); and symbiotic rhizosphere organism activity (Coleman et al. 1983, Ingham et al. 1985). The defoliation resistance mechanisms accelerate growth rates of replacement leaves and shoots, increase photosynthetic capacity of remaining mature leaves, increase allocation of carbon and nitrogen, increase secondary tiller development from axillary buds, and increase conversion of soil organic nitrogen into plant usable mineral nitrogen.

Defoliation by grazing that removes 25% to 33% of the leaf area of perennial grass tillers at phenological growth stages between the three and a half new leaf stage and the flower (anthesis) stage is needed to trigger these beneficial mechanisms (Manske 1999, 2007), however, a threshold quantity of 100 pounds per acre or greater of mineral nitrogen processed by the rhizosphere organisms is required for full activation of the defoliation resistance mechanisms in grazed grass tillers (Manske 2009, 2010).

Perennial grass plants and rhizosphere organisms interact in the narrow zone of soil around grass roots. The rhizosphere contains bacteria, protozoa, nematodes, mites, springtails, and endomycorrhizal fungi (Elliot 1978, Anderson et al. 1981, Harley and Smith 1983, Curl and Truelove 1986, Whipps 1990, Campbell and Greaves 1990). The grass plants release carbon compounds (Campbell and Greaves 1990), including sugars, through the roots into the rhizosphere, and the soil microorganisms release mineral nitrogen that the plants absorb (Ingham et al. 1985, Clarholm 1985, Biondini et al. 1988, Frederick and Klein 1994, Frank and Groffman 1998). The endomycorrhizal fungi also provide phosphorus, other mineral nutrients, and water that the plant needs for growth (Moorman and Reeves 1979, Harley and Smith 1983, Allen and Allen 1990, Koide 1993, Marschner and Dell 1994, Smith and Read 1997). Activity of the soil microorganisms increases with the availability of carbon compounds in the rhizosphere (Curl and Truelove 1986, Whipps 1990), and the elevated microorganism activity results in an increase in mineral nitrogen available to the grass plant (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005).

Grazing lead tillers between the three and a half new leaf stage and the flower stage (Manske 1999) increases the quantity of carbon compounds the defoliated plants release into the rhizosphere (Hamilton and Frank 2001). The increase in mineral nitrogen produced by elevated rates of microorganism activity allows the plant to accelerate growth and recover more quickly from defoliation. This beneficial activity does not occur when grazing is conducted during the middle and late growth stages of grass plants (Manske 2000a, 2007).

The cause of degradation of prairie ecosystems is antagonistic management practices that are not coordinated with plant phenological growth stages and do not meet the biological requirements of the perennial grass plants and the rhizosphere organisms. Ecosystem deterioration starts with management caused reductions in the quantity of plant carbon exudates released into the rhizosphere;

reduced carbon exudates causes a decrease in rhizosphere organism biomass and activity; reduced rhizosphere organism vitality causes a reduction in the quantity of soil organic nitrogen converted into mineral nitrogen. Decreases in the amount of available mineral nitrogen in the ecosystem causes reductions in grass herbage biomass production and causes decreases in plant density (basal cover). When the quantity of mineral nitrogen drops below 100 pounds per acre, the defoliation resistance mechanisms fail to be activated and plant recovery from grazing is incomplete (Manske 2009, 2010). In addition, the water use efficiency processes cease in grass plants growing in ecosystems with less than 100 lbs/ac available mineral nitrogen causing herbage biomass production to be reduced by 49.6% (Wight and Black 1972, 1979). As degradation continues, numerous large bare spaces between grass plants are created in the plant community. These open spaces are ideal habitat for growth of opportunistic “weedy” plant species. The composition of plant species changes with decreases in the desirable species and increases in less desirable species, and later with increases in undesirable species. The change in plant composition from desirable to undesirable species is actually the symptom of ecosystem degradation; the fundamental degradation is the diminishment of ecosystem biogeochemical processes and the reduction of available mineral nitrogen below 100 lbs/ac. The degree of plant species change lags behind the degree of ecosystem biogeochemical degradation.

The greatest antagonistic effects to prairie ecosystems occur from long-term nondefoliation (idle) management that withholds defoliation from a grassland ecosystem. Nondefoliation management results in an accumulation of standing dead leaves that shade lower leaves, increasing the rate of leaf senescence and reducing the rate of photosynthesis, that causes a decrease in the supply of carbohydrates, resulting in a reduction in growth of new leaves and roots (Langer 1972, Briske and Richards 1995). Shading increases grass tiller mortality and reduces grass density (Grant et al. 1983). Reduction of root biomass (Whitman 1974, Brand and Goetz 1986) reduces active root length for interaction with rhizosphere organisms and causes a decrease in absorption of water and nutrients from the soil. Lack of defoliation greatly reduces the quantity of plant carbon exudated into the rhizosphere reducing organism biomass and activity causing a reduction in conversion of soil organic nitrogen into mineral nitrogen.

Under nondefoliation management, dead leaves remain standing for several years. Standing dead plant material not in contact with soil does not decompose through microbial activity. The dead material breaks down slowly as a result of leaching and weathering. A thick mulch layer builds up that modifies soil temperatures, inhibits water infiltration, and retains increasing portions of ecosystem nutrients reducing the quantities of soil organic carbon and nitrogen. Reduced sunlight from shading and reduced quantities of hydrogen, carbon, and nitrogen in the soil, severely reduces the rates of nutrient cycles and biogeochemical processes causing further reductions in leaf growth, tiller leaf area, and grass herbage biomass production. Plant community degradation by nondefoliation promotes changes in composition towards increases in shade-tolerant and shade-adapted replacement species (Manske 2008a).

Prairie ecosystems consist of three components: grass plants, rhizosphere microorganisms, and large grazing herbivores. All three components must be present at sufficient quantities in order for the ecosystem biogeochemical processes to function properly during each growing season. Removal of the large herbivores for one growing season starts the degeneration processes. Degradation of prairie ecosystems caused by nondefoliation management occurs slowly, however, the degree of deterioration to ecosystem biogeochemical processes and plant community structure descends magnitudes greater than any degradation caused by antagonistic grazing management practices (Manske 2008a).

Traditional grazing management practices that are not coordinated with plant phenological growth stages and do not meet the biological requirements of the perennial grass plants and the rhizosphere organisms are detrimental to prairie ecosystems. The deferred grazing, 6.0 month seasonlong, and 4.5 month seasonlong management strategies are antagonistic to rhizosphere organism activity, ecosystem biogeochemical processes, and the nitrogen cycle by causing retardation in the quantity of plant carbon exudation into the rhizosphere. The rhizosphere volume diminishes to levels with insufficient organism biomass and activity to convert soil organic nitrogen into available mineral nitrogen at the threshold rates of 100 lbs/ac. The low rhizosphere volume on the deferred grazing strategy converts an extremely low quantity of mineral nitrogen at 31.2 lbs/ac. The low rhizosphere volume of 49.8 ft^3/ac on the 6.0-m seasonlong grazing strategy converts a low quantity of mineral nitrogen at 62.0 lbs/ac. The low rhizosphere volume of 67.6

ft^3/ac on the 4.5-m seasonlong grazing strategy converts a low quantity of mineral nitrogen at 76.7 lbs/ac (Manske 2008b). The defoliation resistance mechanisms are not activated on prairie ecosystems managed with traditional grazing practices that process mineral nitrogen at rates less than 100 lbs/ac, even if the grass tillers are defoliated at the proper phenological growth stages (Manske 2009, 2010). Without help from compensatory physiological processes and from vegetative reproduction of secondary tillers from axillary buds, desirable native grass tillers cannot fully recover from defoliation by grazing; the grass density and grass herbage biomass production progressively decrease and less desirable replacement species backfill as open spaces develop.

Management strategies that defer grazing until after the flowering stage were intended to enhance sexual reproduction and increase the quantity of seeds produced. However, deferred grazing causes a decrease in native grass plant density (Sarvis 1941, Manske et al. 1988). Most young grass plants in grassland ecosystems start not as seedlings but as vegetative tillers that grow from axillary buds on the crowns of an established plant. These vegetative tillers make up the majority of the plant population because they have a competitive advantage over seedlings. Tillers initially draw support from the root systems of parent tillers, while seedlings must rely on their own less-developed structures.

Tiller development from axillary buds is regulated by lead tillers (Briske and Richards 1995), through a process called lead tiller dominance. The lead tillers produce an inhibitory hormone that prevents the growth hormone from activating growth within axillary buds (Briske and Richards 1995). Reduction of the amount of the inhibitory hormone in the plant allows the growth hormone to activate cell growth in multiple axillary buds (Briske and Richards 1994). With that inhibitory hormone reduced, the growth hormone stimulates vegetative reproduction (Murphy and Briske 1992, Briske and Richards 1994), and secondary tillers develop from the axillary buds (Langer 1972). Grazing that removes 25% to 33% of the young leaf tissue from the aboveground portion of lead tillers after the three and a half new leaf stage and before the flower stage increases activation of vegetative tillers from axillary buds (Manske 2007).

All grass species in the Northern Plains have strong lead tiller dominance except Kentucky bluegrass and meadow bromegrass, which have low levels of inhibitory hormones and relatively higher levels of tiller development. Plants with these growth characteristics have greater demand for water than grasses with strong lead tillers and cease growth processes during minor water deficiency periods.

Beneficial grass plant response to grazing depends on the timing of defoliation. Grazing grass plants prior to the three and a half new leaf stage negatively affects grass growth (Manske 2000b). Early seasonal growth of grass plants depends on carbohydrates stored in the roots, rhizomes, and stem bases (Trlica 1977), and prematurely grazed plants are unable to replenish adequate amounts of carbohydrates to support active growth (Coyne et al. 1995, Manske 1999). Grazing after the three and a half new leaf stage and before the flower stage allows plants to establish sufficient leaf area to produce adequate photosynthetic assimilates to meet leaf growth requirements and allows all leaf bud primordia in the apical meristem to develop into leaf buds (Manske 1999).

If no defoliation occurs before the flower stage, as on a deferred grazing strategy, the lead tiller inhibits vegetative tiller development until the inhibitory hormone production naturally declines during the flower stage. This hormone reduction permits one axillary bud to grow and develop into a secondary tiller, which in turn produces inhibitory hormones that prevent growth of the other six to eight axillary crown buds (Mueller and Richards 1986). These dormant axillary buds are never activated and become senescent with the lead tiller. The lack of defoliation of lead tillers prior to the flower stage diminishes recruitment of vegetative tillers, leading to decreased plant density and reduced rhizosphere organism activity; this reduction results in decreased conversion of soil organic nitrogen into mineral nitrogen. No evidence has been found to suggest that grazing the lead tiller after it has reached the flower stage has beneficial stimulatory effects on vegetative tiller development or rhizosphere organism activity (Manske 2000a).

Late season grazing after mid October and early season grazing before the three and a half new leaf stage are antagonistic to native perennial grasses. Late grazing is not harmful to senescent lead tillers that produced seeds that growing season. Usually around 25% of the tiller population reaches the reproductive phenological growth stage, however, it can vary from 5% to 50% of the tiller population. The other tillers that did not produce seeds will overwinter and resume active growth during the subsequent growing season. Late season grazing of carryover tillers causes decreased tiller numbers, reduced total basal area, and reduced quantities of herbage biomass produced (Olson and Richards 1988, Coyne et al. 1995). Winter survival of carryover tillers depends on having adequate carbohydrate reserves which is closely related to the amount of active leaf material remaining on each tiller during the winter hardening process, that occurs between mid August and mid October. The crown, portions of the root system, and some leaf tissue remain active and maintain physiological processes throughout the winter using stored carbohydrates. Depletion of the carbohydrates reserves before spring causes tiller death, “winter kill”.

During early spring, portions of the carryover tillers’ leaves from the previous year that have intact cell walls regreen with chlorophyll and provide crucial photosynthetic product for new leaf growth (Briske and Richards 1995). New growing leaves draw carbohydrates from the carryover older leaves until maintenance and growth requirements can be met by the new leaves (Langer 1972, Coyne et al. 1995). Removal of leaf matreial by grazing from grass tillers not yet at the three and a half new leaf stage deprives the new tillers of foliage needed for photosynthetic product and causes a demand on the low levels of carbohydrate reserves that results in a reduction of the herbage biomass production well below potential quantities later in the growing season (Campbell 1952, Rogler et al. 1962, Manske 2000b).

The twice-over rotation grazing management system is the biologically effective management strategy that is coordinated with grass phenological growth stages and meets the biological requirements of the perennial grass plants and soil organisms by applying defoliation treatment to grass plants at the appropriate growth stages that activate the defoliation resistance mechanisms and stimulate the symbiotic rhizosphere microorganisms biomass and activity (Manske 1999, 2000a; Gorder, Manske, Stroh 2004). The increased rhizosphere activity results in an increased quantity of available mineral nitrogen. The high rhizosphere volume of 227.1 ft^3/ac on the twice-over rotation grazing strategy converts a high quantity of mineral nitrogen at 177.8 lbs/ac (Manske 2009, 2010).

The twice-over rotation grazing management system uses three to six pastures. Every pasture is grazed during two periods per growing season. Each pasture is grazed for 7 to 17 days during the first period, the 45-day interval from 1 June to 15 July. The length of the first period on each pasture is the same percentage of 45 days as the percentage of the total season's grazeable forage each pasture contributes (Manske 2000a). During the second period, after mid July and before mid October, each pasture is grazed for double the number of days it was grazed during the first period. Livestock are removed in mid October.

The coordinated defoliation improves plant health and stimulates biological and ecological processes within grass plants and the ecosystem so that beneficial changes to plant growth, soil organisms, and biogeochemical cycles in the ecosystem result (Manske 2000a). During the first grazing period, grasses are between the three and a half new leaf and flower stages, the stages of plant development at which grazing stimulates the defoliation resistance mechanisms that increase tillering from axillary buds and enhance rhizosphere organism activity increasing the conversion of soil organic nitrogen into mineral nitrogen. Increased vegetative reproduction by tillering contributes to the development of greater plant basal cover and to the production of greater grass herbage weight; increased activity of the soil organisms in the rhizosphere supplies the plant with greater quantities of nutrients to support additional growth (Manske 2000a).

Restoration of degraded prairie ecosystems requires implementation of a biologically effective grazing management strategy that meets the biological requirements of the perennial grass plants and rhizosphere organisms, and that is coordinated with perennial grass phenological growth stages. Proper defoliation during the first grazing period removes 25% to 33% of the leaf area of grass tillers between the three and a half new leaf stage and the flower stage. This defoliation by grazing treatment increases the quantity of plant carbon exudates released into the rhizosphere causing an increase in the biomass and activity of the rhizosphere organisms that results in an increase in the quantity of soil organic nitrogen converted into mineral nitrogen. Increases in the amount of available mineral nitrogen processed by rhizosphere organisms in the degraded prairie ecosystem results in increases in grass herbage biomass production and increases in plant density (basal cover) of the desirable native grass species. When the quantity of mineral nitrogen increases to 100 pounds per acre or greater, the defoliation resistance mechanisms can be fully activated that accelerate growth rates of replacement leaves and shoots, increase photosysnthetic capacity of remaining mature leaves, increase allocation of carbon and nitrogen, and increase secondary tiller development from axillary buds. The water use efficiency processes also are activated in grass plants resulting in an increase of 50.4% in herbage biomass production per inch of precipitation received. As restoration continues, native perennial grass species composition increases in the plant community. The native grasses out compete the less desirable and the undesirable species for space and nutrient resources because of the advantages provided by the symbiotic relationship with the rhizosphere organisms. The restoration of the native plant species composition lags behind the restoration of the prairie ecosystem biogeochemical processes and the recovery of the nitrogen cycle.

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Literature Cited

Allen, E.B., and M.F. Allen. 1990. The mediation of competition by mycorrhizae in successional and patchy environments. p. 307-389. in J.B. Grace and D. Tilman (eds.). Perspectives on plant competition. Academic Press Inc., San Diego, CA.

Anderson, R.V., D.C. Coleman, C.V. Cole, and E.T. Elliott. 1981. Effect of nematodes Acrobeloides sp. and Mesodiplogaster lheritieri on substrate utilization and nitrogen and phosphorus mineralization. Ecology 62:549-555.

Biondini, M., D.A. Klein, and E.F. Redente. 1988. Carbon and nitrogen losses through root exudation by Agropyron cristatum, A. smithii, and Bouteloua gracilis. Soil Biology and Biochemistry 20:477-482.

Bird, S.B., J.E. Herrick, M.M. Wander, and S.F. Wright. 2002. Spatial heterogeneity of aggregate stability and soil carbon in semi-arid rangeland. Environmental Pollution 116:445-455.

Brand, M.D., and H. Goetz. 1986. Vegetation of exclosures in southwestern North Dakota. Journal of Range Management 39:434-437.

Briske, D.D. 1991. Developmental morphology and physiology of grasses. p. 85-108. in R.K. Heitschmidt and J.W. Stuth (eds.). Grazing management: an ecological perspective. Timber Press, Portland, OR.

Briske, D.D., and J.H. Richards. 1994. Physiological responses of individual plants to grazing: current status and ecological significance. p. 147-176. in M. Vavra, W.A. Laycock, and R.D. Pieper (eds.). Ecological implications of livestock herbivory in the west. Society for Range Management, Denver, CO.

Briske, D.D., and J.H. Richards. 1995. Plant response to defoliation: a physiological, morphological, and demographic evaluation. p. 635-710. in D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Burrows, R.L., and F.L. Pfleger. 2002. Arbuscular mycorrhizal fungi respond to increasing plant diversity. Canadian Journal of Botany 80:120-130.

Campbell, J.B. 1952. Farming range pastures. Journal of Range Management 5:252-258.

Campbell, R., and M.P. Greaves. 1990. Anatomy and community structure of the rhizosphere. p. 11-34. in J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

Clarholm, M. 1985. Interactions of bacteria, protozoa, and plants leading to mineralization of soil nitrogen. Soil Biology and Biochemistry 17:181-187.

Coleman, D.C., C.P.P. Reid, and C.V. Cole. 1983. Biological strategies of nutrient cycling in soil ecosystems. Advances in Ecological Research 13:1-55.

Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995. Carbon and nitrogen dynamics in range plants. p. 59-167. in D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Curl, E.A., and B. Truelove. 1986. The rhizosphere. Springer-Verlag, New York, NY.

Driver, J.D., W.E. Holben, and M.C. Rillig. 2005. Characterization of glomalin as a hyphal wall component of arbuscular mycorrhizal fungi. Soil Biology and Biochemistry 37:101-106.

Elliot, E.T. 1978. Carbon, nitrogen and phosphorus transformations in gnotobiotic soil microcosms. M.S. Thesis. Colorado State University, Ft. Collins, CO.

Frank, D.A., and P.M. Groffman. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. Ecology 79:2229-2241.

Frederick, B.A., and D.A. Klein. 1994. Nitrogen effects on rhizosphere processes of range grasses from different successional seres. Plant and Soil 161:241-250.

Gorder, M.M., L.L. Manske, and T.L. Stroh. 2004. Grazing treatment effects on vegetative tillering and soil rhizospheres of western wheatgrass. NDSU Dickinson Research Extension Center. Range Research Report DREC 04-1056. Dickinson, ND. 13p.

Grant, S.A., G.T. Barthram, L. Torvell, J. King, and H.K. Smith. 1983. Sward management, lamina turnover and tiller population density in continuously stocked *Lolium perenne*-dominated swards. Grass and Forage Science 38:333-344.

Hamilton, E.W., and D.A. Frank. 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82:2397-2402.

Harley, J.L., and S.E. Smith. 1983. Mycorrhizal symbiosis. Academic Press, New York, NY.

Ingham, R.E., J.A. Trofymow, E.R. Ingham, and D.C. Coleman. 1985. Interactions of bacteria, fungi, and the nemotode grazers: effects of nutrient cycling and plant growth. Ecological Monographs 55:119-140.

Klein, D.A., B.A. Frederick, M. Biondini, and M.J. Trlica. 1988. Rhizosphere microorganism effects on soluble amino acids, sugars, and organic acids in the root zone of Agropyron cristatum, A. smithii, and Bouteloua gracilis. Plant and Soil 110:19-25.

Koide, R.T. 1993. Physiology of the mycorrhizal plant. p. 33-54. in D.S. Ingram and P.H. Williams (eds.). Mycorrhiza synthesis. Academic Press, London, UK.

Langer, R.H.M. 1972. How grasses grow. Edward Arnold, London, Great Britain.

Manske, L.L., W.T. Barker, and M.E. Biondini. 1988. Effects of grazing management treatments on grassland plant communities and prairie grouse habitat. USDA Forest Service. General Technical Report RM-159. p. 58-72.

Manske, L.L. 1999. Can native prairie be sustained under livestock grazing? p. 99-108. in J. Thorpe, T.A. Steeves, and M. Gollop (eds.). Proceedings of the Fifth Prairie Conservation and Endangered Species Conference. Provincial Museum of Alberta. Natural History Occasional Paper No. 24. Edmonton, Alberta, Canada.

Manske, L.L. 2000a. Management of Northern Great Plains prairie based on biological requirements of the plants. NDSU Dickinson Research Extension Center. Range Science Report DREC 00-1028. Dickinson, ND. 12p.

Manske, L.L. 2000b. Grazing before grass is ready. NDSU Dickinson Research Extension Center. Range Management Report DREC 00-1032. Dickinson, ND. 6p.

Manske, L.L. 2007. Biology of defoliation by grazing. NDSU Dickinson Research Extension Center. Range Management Report DREC 07-1067. Dickinson, ND. 25p.

Manske, L.L. 2008a. Effects from long-term nongrazing. NDSU Dickinson Research Extension Center. Range Management Report DREC 08-1011c. Dickinson, ND. 8p.

Manske, L.L. 2008b. Grazing and burning treatment effects on soil mineral nitrogen and rhizosphere volume. NDSU Dickinson Research Extension Center. Range Research Report DREC 08-1066b. Dickinson, ND. 15p.

Manske, L.L. 2009. Grass plant responses to defoliation. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1074. Dickinson, ND. 47p.

Manske, L.L. 2010. Evaluation of the defoliation resistance mechanisms influence on vegetative tiller initiation and tiller density. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1076. Dickinson, ND. 13p.

Marschner, H., and B. Dell. 1994. Nutrient uptake in mycorrhizal symbiosis. Plant and Soil 159:89-102.

McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist 113:691-703.

McNaughton, S.J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329-336.

Moorman, T., and F.B. Reeves. 1979. The role of endomycorrhizae in revegetation practices in the semi-arid west. II. A bioassay to determine the effect of land disturbance on endomycorrhizal populations. American Journal of Botany 66:14-18.

Mueller, R.J., and J.H. Richards. 1986. Morphological analysis of tillering in Agropyron spicatum and Agropyron desertorum. Annals of Botany 58:911-921.

Murphy, J.S., and D.D. Briske. 1992. Regulation of tillering by apical dominance: chronology, interpretive value, and current perspectives. Journal of Range Management 45:419-429.

Olson, B.E., and J.H. Richards. 1988. Spatial arrangement of tiller replacement in *Agropyron desertorum* following grazing. Oecologia 76:7-10.

Richards, J.H., R.J. Mueller, and J.J. Mott. 1988. Tillering in tussock grasses in relation to defoliation and apical bud removal. Annals of Botany 62:173-179.

Rillig, M.C., S.F. Wright, and V.T. Eviner. 2002. The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. Plant and Soil 238:325-333.

Rogler, G.A., R.J. Lorenz, and H.M. Schaaf. 1962. Progress with grass. North Dakota Agricultural Experiment Station. Bulletin 439. 15p.

Sarvis, J.T. 1941. Grazing investigations on the Northern Great Plains. North Dakota Agricultural Experiment Station. Bulletin 308. Fargo, ND.

Smith, S.E., and D.J. Read. 1997. Mycorrhizal symbiosis. Academic Press, San Diego, CA.

Trlica, M.J. 1977. Distribution and utilization of carbohydrate reserves in range plants. p. 73-97. in R.E. Sosebee (ed.). Range plant physiology. Range Science Series No. 4. Society for Range Management, Denver, CO.

Whipps, J.M. 1990. Carbon economy. p. 59-97. in J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

Whitman, W.C. 1974. Influence of grazing on the microclimate of mixed grass prairie. p. 207-218. *in* Plant Morphogenesis as the basis for scientific management of range resources. USDA Miscellaneous Publication 1271.

Wight, J.R., and A.L. Black. 1972. Energy fixation and precipitation use efficiency in a fertilized rangeland ecosystem of the Northern Great Plains. Journal of Range Management 25:376-380.

Wight, J.R., and A.L. Black. 1979. Range fertilization: plant response and water use. Journal of Range Management 32:345-349.

Degradation and Biological Restoration of Mixed Grass Prairie Ecosystems

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Strategies used to manage mixed grass prairie ecosystems that are antagonistic to grass plant and soil organism biological requirements cause diminished activation of the defoliation resistance mechanisms within grass plants, reduced productiveness of ecosystem biogeochemical processes, and decreased competitiveness of grass plant resource uptake processes resulting in ecosystem degradation. Symptoms of degraded ecosystem processes are visually expressed as changes in the vegetation composition. The severity of ecosystem degradation corresponds to the severity and duration of the management strategy antagonism. The functionality of ecosystem processes descend on a regressive continuum of deterioration from an extremely healthy ecosystem downwards to a disfunctional ecosystem with great reductions of native grasses, considerable decreases of desirable forbs, enormous increases of introduced domesticated grasses, remarkable increases of woody shrubs and trees, and excessive quantities of standing dead and litter.

Degraded mixed grass prairie ecosystem processes show symptoms of three major stages of vegetation deterioration: A) mixed grass prairie ecosystems with highly degraded processes at increasing intensities have plant communities dominated by native grasses at decreasing condition, B) mixed grass prairie ecosystems with severely degraded processes have plant communities dominated by invasive domesticated grasses, and C) mixed grass prairie ecosystems with extremely degraded processes have plant communities invaded by or dominated by woody shrubs. Biological restoration of the processes within mixed grass prairie ecosystems showing symptoms of degradation at the three major stages of vegetation deterioration is possible with implementation of biologically effective management plus the addition of specific management practices needed to correct the additional specific problems created by each of the increasing stages of deterioration.

Mixed grass prairie communities are complex ecosystems consisting of numerous interactive biotic (living) and abiotic (nonliving) components. The biotic components are the plants, soil organisms, and large grazing graminivores that have biological and physiological requirements. The abiotic components include the essential major elements of carbon, hydrogen, and nitrogen in the presence of sunlight that have transformable characteristics through biogeochemical processes. Prairie ecosystems are functioning units of coacting biotic organisms interacting with the abiotic components and the environment. In order for all the ecosystem components to interact and function at potential levels, the defoliation resistance mechanisms within the grass plants, the ecosystem biogeochemical processes, and the grass plant resource uptake processes require activation through partial defoliation of 25% to 33% of the leaf material of grass lead tillers at phenological growth stages between the 3.5 new leaf stage and the flower stage by large grazing graminivores (Manske 2010a, 2010b). Partial defoliation by grazing graminivores managed by the biologically effective twice-over rotation strategy coordinates defoliation events with grass phenological growth stage, meets the nutritional requirements of the grazing animals, meets the biological requirements of the grass plants and the rhizosphere organisms, and activates the ecosystem processes to function at potential levels. Grazing animals are essential annual growing season components of mixed grass prairie ecosystems. If any of the numerous processes are not functioning at potential level, the ecosystem does not function at potential level (Manske and Schneider 2012a). When the ecosystem is not functioning at the potential level, the ecosystem is functioning at a degraded level.

Degradation from Traditional Grazing Practices

Ecosystem processes function at some degree less than potential level each growing season that grazing defoliation is managed with traditional practices that are based on grassland use as forage for livestock. Soon after the ecosystem processes fail to function properly, the belowground components begin to deteriorate. The native grass live root biomass decreases (Whitman 1974), the defoliation resistance mechanisms within grass plants diminish, the ecosystem biogeochemical processes decline, and the competitiveness of grass plant resource uptake deteriorates (Manske 2011b).

The reduction of live root surface area causes a decrease in active root length for interaction with symbiotic rhizosphere organisms and causes a decrease in absorption of water and nutrients from the soil. Reduction of active root biomass and diminishment of grass plant health vigor result 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 (Kochy 1999, Kochy and Wilson 2000). The loss of active root length is a contributing factor in the reduction of rhizosphere biomass. The primary cause for the reduction in rhizosphere biomass is, however, the great reduction in the quantity of carbohydrates exuded from the grass roots into the rhizosphere zone. The antagonistic defoliation by grazing managed by traditional practices greatly reduces the quantity of short carbon chain energy exuded from the grass roots into the rhizosphere; this low amount of simple carbon compounds is not enough to sustain an adequate rhizosphere biomass. A small biomass of rhizosphere organisms mineralize small quantities of nitrogen and other essential elements (Coleman et al. 1983, Klein et al. 1988).

Rhizosphere organism biomass and activity are limited by access to simple carbon chain energy (Curl and Truelove 1986) because the microflora trophic levels lack chlorphyll and have low carbon (energy) content. Partial defoliation by large grazing graminivores of grass lead tillers at vegetative phenological growth stages is required to cause greater quantities of exudates containing simple carbon compounds to be released through the grass roots into the rhizosphere. Biomass and activity of the microorganisms increase with the increase in availability of energy from simple carbon compounds in the rhizosphere. The increase in rhizosphere organism biomass and activity causes an increase in mineralization of nitrogen and other essential elements. The severity of antagonism to ecosystem processes and the degree of resulting deficiencies in mineral nitrogen and other essential elements are not the same for all traditional grazing practices.

The traditional grazing management practice of 4.5 month seasonlong is grazed at moderate stocking rates on native grasslands between early June and mid October and is moderately antagonistic to mixed grass prairie ecosystems. After 20 years, the plant communities had been degraded 23% and were dominated by native grasses. The mean monthly grazing season live herbage biomass production was 1280 lbs/ac with 55.1% native grasses, 30.6% upland sedges, and 14.5% forbs. The rhizosphere volume was reduced to 67.6 ft ^{3}/ac (29.8% of potential volume) and the available mineral nitrogen was reduced to 76.7 lbs/ac (Manske 2011a) (table 1).

The traditional grazing management practice of 6.0 month seasonlong is grazed at slightly heavier than moderate stocking rates on native grasslands between mid May and mid November and is highly antagonistic to mixed grass prairie ecosystems. After 20 years, the plant communities had been degraded 38% and were dominated by native grasses. The mean monthly grazing season live herbage biomass production was 906 lbs/ac with 53.8% native grasses, 27.1% upland sedges, and 19.2% forbs. The rhizosphere volume was reduced to 49.8 ft ^{3}/ac (21.9% of potential volume) and the available mineral nitrogen was reduced to 61.6 lbs/ac (Manske 2011a) (table 1).

The traditional grazing management practice of long duration 7.0 to 8.0 month seasonlong is grazed at moderate stocking rates on native grasslands starting in early May and continuing until late December or until inclement weather prevents late season grazing and is severely antagonistic to mixed grass prairie ecosystems. After 75 years, the plant communities had been degraded 57% and were dominated by native grasses; woody plant cover had invaded only 0.03% of the grazed area. The aboveground vegetation consisted of 23.9% standing dead and litter and 76.1% live herbage biomass. The peak growing season live herbage biomass was 1719 lbs/ac with 10.3% invasive domesticated grasses, 64.0% native grasses, 15.7% upland sedges, and 10.1% forbs. The rhizosphere biomass was reduced to 154.7 kg/m^{3} (38.1% of potential weight) and the available mineral nitrogen was reduced to 42.4 lbs/ac (Manske and Schneider 2012a) (table 1).

The traditional grazing management practice of 4.0 month deferred, delays grazing until grass tillers are mature, is grazed at moderate to heavy stocking rates on native grasslands between mid July and mid November and is extremely antagonistic to mixed grass prairie ecosystems. After 50 years, the plant communities had been severely degraded 69%. The great loss of native grasses created large open spaces and the deferred grazed areas became dominated by Kentucky bluegrass, smooth bromegrass, and western snowberry. Woody shrub cover had invaded greater than 50% of the area. The aboveground vegetation consisted of 32.5% standing dead, 32.1% current year shrub growth, and 35.4% live herbage biomass. The peak growing season live herbage biomass was 891 lbs/ac with 20.7% invasive domesticated grasses, 25.5% native grasses, 25.2% upland sedges, and 28.6% forbs. The rhizosphere biomass was greatly reduced and the available mineral nitrogen was reduced to 31.2 lbs/ac (Manske 2007a, 2011a) (table 1).

The traditional grazing management practice of long duration repeat seasonal is grazed at heavier than moderate stocking rates on native grasslands starting as early in May as possible, before the grass lead tillers reach the 3.5 new leaf stage, continuing until inclement weather prevents late season grazing and is extremely antagonistic to mixed grass prairie ecosystems. After more than 30 years, the plant communities had been severely degraded. The great loss of native grasses created large open spaces and the heavily grazed long duration pastures became dominated by invasive Kentucky bluegrass and western snowberry. The mean herbage biomass was 802 lbs/ac. The rhizosphere biomass was greatly reduced and the available mineral nitrogen was low.

Degradation from Nondefoliation

Nondefoliation management by complete rest of mixed grass prairie ecosystems is not a revitalizing inactivity. Removing graminivores from grassland ecosystems to provide rest from grazing is a devitalizing activity that results in decreased rhizosphere organism biomass causing deficiencies in mineral nitrogen and other essential elements, and that results in decreased sunlight intensity and soil water causing deficiencies in fixed carbon and vital organic compounds.

An evolutionary survival mechanism of grass plants in response to partial defoliation and the loss of leaf area as forage to grazing graminivores is the production of double the quantity of leaf biomass than needed for normal plant growth and maintenance (Crider 1955, Coyne et al. 1995). This survival mechanism does not stop upon removal of grazing graminivores. Without grazing graminivores to remove half of the annual herbage production, the surplus leaf material accumulates rapidly and changes from an asset to a detriment. The accumulation of nondefoliated live and standing dead leaves of grasses reduce light penetration below native grass light saturation points (Peltzer and Kochy 2001). Native grasses have high light saturation points and require near full sunlight. Warm season grasses have higher light saturation points then cool season grasses (Kochy 1999, Kochy and Wilson 2000). Shading reduces native warm season grasses more than native cool season grasses. Introduced cool season domesticated grasses have lower light saturation points than native grasses, permitting domesticated grasses to live in low light conditions.

Low amounts of sunlight reaching native grass leaves decrease the rate of photosynthesis, which reduces the quantity of atmospheric carbon dioxide fixed, reducing the quantity of simple carbohydrates produced (Coyne et al. 1995). Low quantities of carbohydrates cause decreases in growth of roots, leaves, and stems, and development of secondary tillers. Low quantities of carbohydrates also cause increases in the rates of leaf senescence and increases in tiller mortality that results in reductions of native grass plant density (basal cover) and reductions of herbage biomass production (Langer 1972, Grant et al. 1983, Briske and Richards 1995).

The rapidly accumulating quantities of standing dead biomass cannot make contact with the soil surface and decompose quickly through microbial activity. The standing dead biomass decreases slowly by leaching and weathering and builds up into a thick mulch layer. Thick mulch effectively blocks sunlight from reaching understory young grass leaves. Thick mulch insulates the soil from warm spring air temperatures preventing heating of cold soil that causes delays in plant and soil organism activity. Thick mulch ties up and holds organic nutrients above the soil surface preventing accession to the soil organic matter which limits nutrient cycling through biogeochemical processes increasing the deficiencies of essential elements. Thick mulch absorbs and holds precipitation for later evaporation preventing the water from infiltrating into the soil diminishing soil water to deficiency quantities (Wright and Bailey 1982, Manske 2000, 2011a). These undesirable modifications to the ecosystem cause decreases in soil microorganism biomass and activity resulting in further reductions in the rates of organic material decomposition (Anderson et al. 1981, Curl and Truelove 1986, Whipp 1990).

Grass plants developed several physiological, biological, and biogeochemical processes early during coevolution with graminivores in response to partial defoliation and the removal of leaf area (McNaughton 1979, 1983; Coleman et al. 1983; Briske 1991; Briske and Richards 1995; Manske 1999). This set of processes are collectively recognized as defoliation resistance mechanisms (Briske 1991, Briske and Richards 1995). Annual partial defoliation by grazing graminivores of grass lead tillers at growth stages between the 3.5 new leaf stage and the flower stage is required to activate the defoliation resistance mechanisms.

Native grass plants need the essential major elements of carbon, hydrogen, and nitrogen in the presence of sunlight for physiological growth processes to produce leaves, stems, roots, and secondary tillers (Manske 2011b). Removal of grazing graminivores from grasslands and the failure to activate the defoliation resistance mechanisms restricts grass plants use of important mechanisms and processes necessary for normal grass growth and development.

The carbon allocated for grass growth after the 3.5 new leaf stage does not come from stored material in the roots but is carbon recently fixed (Richards and Caldwell 1985, Coyne et al. 1995, Briske and Richards 1995). The carbon comes from atmospheric carbon dioxide which composes about 0.03% of the gasses in the atmosphere and exists at concentrations of around 370 to 385 mg/kg. Atmospheric carbon dioxide is not limiting on rangelands. The carbon dioxide is fixed with hydrogen from soil water during the process of photosynthesis which converts energy from sunlight into chemical energy and assimilates simple carbohydrates. However, when nondefoliated live and standing dead leaves of grasses reduce sunlight reaching understory grass leaves, photosynthetic rates are greatly reduced and available fixed carbon becomes deficient.

The hydrogen allocated for grass growth comes from soil water absorbed through the roots. Soil water is infiltrated precipitation. In western North Dakota, the perennial plant growing season months have a long-term periodicity rate of water deficiency conditions at 32.7%, for a mean of 2.0 months with water deficiency per growing season (Manske et al. 2010). The thick mulch that builds up on nondefoliation managed grasslands causes additional soil water problems. Thick mulch intercepts a portion of the precipitation inhibiting infiltration. The thicker the mulch, the greater the quantity of the precipitation absorbed. Absorption of the precipitation by the mulch causes a deficiency in soil water further inhibiting carbon assimilation.

The nitrogen allocated for grass growth can be mobilized from shoot and root tissue (Briske and Richards 1995) when the preferential source of mineral nitrogen recently converted from soil organic nitrogen by active rhizosphere organisms is low. Low quantities of available soil mineral nitrogen below 100 lbs/ac is the major limiting factor of herbage growth on rangelands (Wight and Black 1979). However, mixed grass prairie soils are not deficient of nitrogen. Most of the nitrogen is immobilized in the soil as organic nitrogen. Untilled grassland soils contain about 3 to 8 tons of organic nitrogen per acre. Soil organic nitrogen must be mineralized by rhizosphere organisms to become plant usable mineral nitrogen. The quantity of rhizosphere organisms is the limiting factor in grassland ecosystems low in mineral nitrogen. Biomass and activity of organisms in the rhizosphere are limited by access to energy from simple carbohydrates which can be exudated from grass lead tillers with partial defoliation by grazing graminivores when grass tillers are at vegetative growth stages after the 3.5 new leaf stage. Available mineral nitrogen becomes extremely deficient when grazing graminivores are removed from a grassland.

Light is radiant energy from the sun and is necessary for photosynthesis. Intensity of sunlight can be greatly reduced by shading from other plants. Nondefoliated live and standing dead leaves of grasses reduce light penetration to a similar degree as shrubs, even though shrub leaves are flat and wide and grass leaves are erect and linear (Kochy 1999). The light levels penetrating the leaf canopy can be about 20% of the light levels above the canopy (Peltzer and Kochy 2001).

Nondefoliation of native grass plants reduces exudation of short carbon chain energy into the rhizosphere to a low level of incidental leakage, reducing biomass and activity of soil organisms, decreasing mineralization processes that cause deficiencies in mineral nitrogen and other essential elements. Failure to remove the double produced leaf biomass annually causes shading that greatly reduces the sunlight intensity reaching native grass leaves, reducing photosynthetic rates that cause deficiencies in available fixed carbon. Accumulation of undecomposed grass leaf material modifies soil temperatures, causes deficiencies in soil water, and causes additional deficiencies in essential elements. The deficiencies of indispensable component resources of carbon, hydrogen, nitrogen, and other essential elements prevent grass plants from synthesizing sufficient quantities of vital carbohydrates, proteins, and nucleic acids. Without sufficient quantities of vital organic compounds native grass plants cannot maintain production of herbage biomass and tiller numbers (Langer 1972, Briske and Richards 1995).

Grasses with long shoots and stalk leaves provide low basal cover and low soil cover. Plant communities with increasing composition of grasses with long shoots and stalk leaves have low ground cover that results in great amounts of soil exposed to erosion and exposed to high levels of solar radiation that causes high rates of soil water transpiration. Grasses with short shoots and basal leaves provide high basal cover and high soil cover. Plant communities with good composition of grasses with short shoots and basal leaves have high ground cover near the soil surface which forms a closed community that protects the soil from erosion and solar radiation. Increases of canopy cover shading by taller live and standing dead leaves reduces the intensity of sunlight reaching the understory leaves of grasses with short shoots and basal leaves causing a disproportional mortality that creates large open spaces in the plant community.

Advanced degradation by antagonistic nondefoliation management of mixed grass prairie communities results in creation of numerous large bare spaces between native grass plants in the plant community. These open spaces, that lack competition from native grasses, are ideal habitat for growth of introduced cool season domesticated grasses like Kentucky bluegrass, and smooth bromegrass, and for growth of other opportunistic "weedy" plant species. These introduced plants have labile roots that break down easily making the nutrients contained in dead roots readily available to support continued growth and expansion of these nonnative plants without assistance from symbiotic rhizosphere organisms. The composition of plant species changes with decreases in the desirable species and increases in less desirable species, and later with increases in undesirable species. The change in plant composition from desirable to undesirable species is actually the symptom of ecosystem degradation; the fundamental degradation is the diminishment of defoliation resistance mechanisms within grass plants, the decrease of ecosystem biogeochemical processes, and the reduction of available mineral nitrogen below 100 lbs/ac. The degree of plant species change lags behind the degree of ecosystem biogeochemical degradation. Nondefoliation management can degrade mixed grass prairie more drastically than poor grazing management.

The nondefoliation management practice of complete rest from grazing removes large graminivores for longer than a decade and is extremely antagonistic to mesic mixed grass prairie ecosystems. After 13 years of nondefoliation, the plant communities at site #1 had been greatly degraded 87%. The 82.0% loss of native grasses with short shoots and basal leaves created large open spaces and the nongrazed areas at site #1 became dominated by invasive smooth bromegrass. The aboveground vegetation biomass consisted of 68.0% standing dead and litter and 32.0% live herbage. The mean nongrazed live herbage biomass was 1630 lbs/ac with 93.9% invasive domesticated grasses, 2.2% native grasses, 2.2% upland sedges, and 1.8% forbs. The rhizosphere biomass was reduced to 54.1 kg/m^3 (13.3% of potential weight) and the available mineral nitrogen was greatly reduced (Manske and Schneider 2012b) (table 1).

The nondefoliation management practice of complete rest from grazing removes large graminivores for longer than a decade and is extremely antagonistic to mesic mixed grass prairie ecosystems. After 13 years of nondefoliation, the plant communities at site #2 had been greatly degraded 81%. The 39.9% loss of native grasses with short shoots and basal leaves created large open spaces and the nongrazed areas at site #2 became dominated by invasive Kentucky bluegrass. The aboveground vegetation biomass consisted of 63.6% standing dead and litter and 36.4% live herbage. The mean nongrazed live herbage biomass was 1645 lbs/ac with 64.8% invasive domesticated grasses, 3.3% native grasses, 22.9% upland sedges, and 9.0% forbs. The rhizosphere biomass was reduced to 78.0 kg/m^3 (19.2% of potential weight) and the available mineral nitrogen was greatly reduced (Manske and Schneider 2012b) (table 1).

The long-term nondefoliation management practice of complete rest from grazing removes large graminivores for longer than multiple decades and is extremely antagonistic to xeric mixed grass prairie ecosystems. After 75 years of nondefoliation, the plant communities at long-term nongrazed areas had been degraded 61%. The 74.4% loss of native grasses with short shoots and basal leaves created large open spaces and the long-term nongrazed areas became dominated by invasive Kentucky bluegrass; woody plant cover had invaded 54.4% of the nongrazed area. The aboveground vegetation biomass consisted of 52.4% standing dead and litter and 47.6% live herbage. The mean nongrazed live herbage biomass was 1713 lbs/ac with 59.8% invasive domesticated grasses, 22.7% native grasses, 7.0% upland sedges, and 10.6% forbs. The rhizosphere biomass was reduced to 127.2 kg/m^3 (31.3% of potential weight) and the available mineral nitrogen was reduced to 39.5 lbs/ac (Manske and Schneider 2012a) (table 1).

Removal of cattle grazing from mixed grass prairie plant communities causes discontinuation of defoliation resistance mechanisms, degeneration of ecosystem biogeochemical processes, depletion of plant species composition with severe reductions of native grasses, excessive increases of standing dead and litter, extreme increases of introduced domesticated grasses, and remarkable increases of woody shrub and tree species.

A remarkably high quantity of woody shrub and tree species and an exceptionally great number of individual woody plants were able to develop on nongrazed mixed grass prairie because the competitive advantage of grasses for belowground resources was diminished in conjunction with the degradation of the native grass plant communities that resulted from removal of grazing defoliation by large graminivores. The existence of a shrub component in a grassland plant community is not an ecological beneficial relationship. Shrubs and grasses are adversarial inhibitive competitors. Grasses and shrubs compete for sunlight, mineral nitrogen, and soil water.

The degree of difference in competitive abilities between prairie grasses and shrubs on the mixed grass prairie was investigated during 1994 to 1998 at the University of Regina, Saskatchewan, with direction from Dr. S.D. Wilson. The grass growth form has competitive advantages over the shrub growth form. The per gram of biomass effects on resource use efficiency are smaller for shrub growth forms than for grass growth forms (Kochy and Wilson 2000). Shrubs must use a portion of the photosynthates produced in the leaves to build and maintain their unproductive woody stems; the result is a great reduction in resource uptake efficiency. Shrubs require 6 times greater aboveground biomass than the grasses before grass production is decreased as a result of competition from the shrubs (Kochy 1999). Grass aboveground biomass is primarily productive photosynthetic leaves; the result is a high resource uptake efficiency. Grasses have a 1.4 times greater per gram of biomass resource efficiency effect than shrubs (Kochy 1999). Grasses on prairie habitat attenuated more light, took up more mineral nitrogen, and took up more soil water per gram of biomass than did shrubs on brush habitat (Kochy 1999, Kochy and Wilson 2000). Because grasses have high root : shoot ratios and no woody stems to maintain; grasses are good competitors for belowground resources and superior competitors for mineral nitrogen. Shrub's taller growth form makes the plants superior competitors for aboveground resources (Kochy and Wilson 2000).

Competition between shrubs and grasses during early stages of shrub expansion into prairie habitat of healthy grasses is primarily for belowground resources of nutrients and soil water; under these initial conditions, grasses have the advantage and the shrubs are suppressed (Kochy and Wilson 2000, Peltzer and Kochy 2001). Competition from healthy grasses also reduces the growth rates of shrub rhizomes and causes high mortality rates of young suckers, preventing expansion into healthy grass communities (Li and Wilson 1998). Seedlings of grasses and shrubs are also unable to compete effectively for resources in healthy established grass plant communities and are suppressed (Peltzer and Kochy 2001). Successful competition of grasses for belowground resources prevents shrubs from becoming established in healthy grass communities. Shrubs can compete for some of the belowground resources only after the grass plants have been degraded by antagonistic management practices.

Following the reduction in grass plant resource competitiveness, establishment of shrubs can occur in degraded grasslands, which frequently starts as clumps (Li and Wilson 1998). The belowground resources previously used by the healthy robust grasses, but 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). After grass competition for belowground resources is reduced, shrub rhizome suckers can regain the faster growth rates and higher survival rates (Li and Wilson 1998) resulting in greater shrub stem densities. As shrub stem density increases, the competition shifts to primarily the aboveground resources of light; under these different degraded conditions, shrubs have the advantage and the grasses are strongly suppressed (Kochy and Wilson 2000).

The increase of woody shrubs and trees in grass communities would have traditionally been explained as a result of fire suppression (Humphrey 1962, Stoddart, Smith, and Box 1975, Wright and Bailey 1982). The greater increase of woody plants into the grass communities of the ungrazed prairie has not been the result of fire suppression. The increased woody plant infestation of the ungrazed prairie has been caused by the greatly reduced competitiveness of the ungrazed grasses for belowground resources of mineral nitrogen and soil water in conjunction with diminution of the defoliation resistance mechanisms and the degradation of the biogeochemical processes in the grass plant communities that resulted from the removal of partial defoliation by large grazing graminivores. The grazed grasses have maintained a greater degree of competitiveness than the ungrazed grasses.

Many ecologists have observed that the repeated occurrence of fire was the force that prevented intrusion of shrubs and trees into grasslands (Weaver 1954, Humphrey 1962, Daubenmire 1974, Stoddart, Smith, and Box 1975, Wright and Bailey 1982), and, the obvious corollary, that suppression of fire has facilitated the invasion of shrubs and trees into grasslands (Humphrey 1962, Stoddart, Smith, and Box 1975, Wright and Bailey 1982, Manske et al. 2006a). However, the presence of fire does not prove that grasslands need or are caused by fire (Heady 1975). In the northern mixed grass prairie, fire cannot prevent the invasion of or cause the removal of shrubs and trees that reproduce by vegetative secondary suckers growing from crown (stem base) or rhizome buds (Wright and Bailey 1982, Manske et al. 2006a, Manske 2006b). Almost all deciduous woody plants growing in the Northern Plains grassland reproduce vegetatively.

The increase of undesirable introduced herbaceous grasses and forbs in grass communities has also often times been explained as a result of fire suppression (Wright and Bailey 1982). Kirsch and Kruse (1972) concluded that the cool season exotic grasses, Kentucky bluegrass and smooth bromegrass, have invaded much of the northern mixed grass prairie in the absence of fire. Seedlings of trees, shrubs, weedy forbs, and introduced grasses cannot become established in healthy functioning grassland ecosystems with grasses that have retained full resource uptake competitiveness (Peltzer and Kochy 2001). Establishment of intrusive seedlings can occur only after the grass communities have been degraded by antagonistic management practices. Furthermore, fire cannot prevent establishment and expansion of undesirable seedlings into degraded grass communities unless the fire frequency suppresses seed production of all invasive species in a region.

Repeated prescibed fire can change the percent composition of the aboveground vegetation biomass in degraded mixed grass prairie invaded by shrubs. The composition of introduced cool season grasses, early succession and weedy forbs, and shrub aerial stems decrease temporarily from four repeated every-other-year prescribed fires (Manske 2007a, 2011a). However, the fundamental problems of low native grass resource uptake competitiveness, diminished defoliation resistance mechanisms, and degraded biogeochemical processes remain in the grassland ecosystems following repeated fire events.

None of the physiological and asexual processes of the defoliation resistance mechanisms within grass plants and none of the biogeochemical processes performed by symbiotic rhizosphere organisms within grassland ecosystems are activated by fire. Fire does not stimulate vegetative reproduction by tillering. Fire does not stimulate endomycorrhizal fungal colonization of perennial grass roots. Fire does not stimulate rhizosphere organism biomass and activity. Fire does not stimulate mineralization of soil organic nitrogen into mineral nitrogen (Manske 2007a, 2011a). Fire does not replace partial defoliation by grazing for management of healthy and productive rangeland ecosystems.

The invasion of shrubs, trees, and undesirable forbs and grasses into degraded grassland communities is not the result of fire suppression. Shrubs, trees, and introduced forbs and grasses can effectively compete for a portion of the belowground resources of nutrients and soil water after the competitiveness of the native grasses has been reduced as a result of degradation of the grass community caused by antagonistic management practices.

Restoration from Biologically Effective Defoliation

Implementation of a biologically effective grazing management strategy that stimulates the defoliation resistance mechanisms will meet the biological and physiological requirements of the biotic components and will stimulate the biogeochemical processes that cycle the abiotic components (Manske 2011b). The three main defoliation resistance mechanisms are: compensatory internal physiological processes, internal vegetative reproduction of secondary tillers from axillary buds, and external symbiotic rhizosphere organism activity (McNaughton 1979, 1983; Coleman et al. 1983; Ingham et al. 1985; Mueller and Richards 1986; Richards et al. 1988; Briske 1991; Murphy and Briske 1992; Briske and Richards 1994, 1995; Manske 1999).

The defoliation resistance mechanisms developed early during the coevolution of grass plants and grazing graminivores (McNaughton 1979, 1983; Coleman et al. 1983; Briske 1991; Briske and Richards 1995; Manske 1999) and are a complex assemblage of biogeochemical and physiological processes that involve intricate interactions among rhizosphere microorganisms, grass plants, and large grazing graminivores. Activation of these mechanisms provides important biological and physiological processes permitting native grasses to produce greater herbage biomass and to increase basal cover; these mechanisms also enable grass plants to replace lost leaf material, to restore disrupted physiological processes, and to vegetatively reproduce secondary tillers from axillary buds after partial defoliation by grazing. The defoliation resistance mechanisms function at variable levels of activation depending on the quantity of available mineral nitrogen in grassland ecosystem soil. When mineral nitrogen is available at 100 lbs/ac or greater, the defoliation resistance mechanisms function at full activation. When mineral nitrogen is available at less than 100 lbs/ac, the defoliation resistance mechanisms function at levels less than full activation (Manske 2009). In addition, the water (precipitation) use efficiency processes decrease in grass plants growing in ecosystems with less than 100 lbs/ac available mineral nitrogen causing herbage biomass production to be reduced by 49.6% (Wight and Black 1972, 1979).

The quantity of available mineral nitrogen in grassland ecosystem soils is dependent on the rate of mineralization of soil organic nitrogen by rhizosphere organisms. The larger the rhizosphere volume and microorganism biomass, the greater the quantity of soil mineral nitrogen converted. Rhizosphere volume and microorganism biomass are limited by access to simple carbohydrates (Curl and Truelove 1986). Healthy grass plants capture and fix carbon during photosynthesis and produce carbohydrates in quantities greater than the amount needed for tiller growth and development (Coyne et al. 1995). Partial defoliation of grass tillers at vegetative phenological growth stages by large grazing graminivores causes greater quantities of exudates containing simple carbohydrates to be released from the grass tillers through the roots into the rhizosphere (Hamilton and Frank 2001). With the increase in availability of carbon compounds in the rhizosphere, the biomass and activity of the microorganisms increases (Anderson et al. 1981, Curl and Truelove 1986, Whipps 1990). The increase in rhizosphere organism biomass and activity results in greater rates of mineralization of soil organic nitrogen converting greater quantities of available mineral nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005). Mineral nitrogen available in quantities of 100 lbs/ac or greater allows defoliated grass tillers full activation of the defoliation resistance mechanisms (Manske 2009). Full activation of the compensatory internal physiological processes within grass plants accelerates growth rates of replacement leaves and shoots, increases photosynthetic capacity of remaining mature leaves, increases allocation of carbon and nitrogen, improves water (precipitation) use efficiency, and increases restoration of biological and physiological processes enabling rapid and complete recovery of partially defoliated grass tillers. Full activation of the asexual internal processes of vegetative reproduction increases secondary tiller development from axillary buds and increases initiated tiller density during the grazing season. Full activation of the external symbiotic rhizosphere organism activity increases mineralization of mineral nitrogen, increases ecosystem biogeochemical cycling of essential elements, and improves belowground resource uptake competitiveness (Wight and Black 1972, 1979; McNaughton 1979, 1983; Coleman et al. 1983; Ingham et al. 1985; Mueller and Richards 1986; Richards et al. 1988; Briske 1991; Murphy and Briske 1992; Briske and Richards 1994, 1995; Manske 1999, 2011b; Kochy and Wilson 2000). Restoration of plant community vegetation composition lags behind restoration of ecosystem processes.

Restoration of degraded mixed grass prairie ecosystems dominated by native grasses can be accomplished by implementation of the twice-over rotation system which is a biologically effective grazing management strategy that coordinates defoliation events with grass phenological growth stages, meets the biological requirements of the plants and soil organisms, and meets the nutritional requirements of the grazing animals. After 20 years, the plant communities had been restored 100% with fully functioning defoliation resistance mechanisms, ecosystem biogeochemical processes, and resource uptake competitiveness. The mean monthly grazing season live herbage biomass production was 1794 lbs/ac with 74.7% native grasses, 14.2% upland sedges, and 11.1% forbs. The rhizosphere volume was increased to 227.1 ft ^{3}/ac and the biomass increased to 406.4 kg/m^3 (100.0% of potential volume and biomass) and the available mineral nitrogen was increased to 177.8 lbs/ac (Manske 2007b, 2011a) (table 1).

Restoration of degraded mesic mixed grass prairie ecosystems at site #1 dominated by smooth bromegrass was attempted by implementation of the twice-over rotation system. Before the grazing treatment started, the aboveground vegetation biomass consisted of 68.0% standing dead and litter and 32.0% live herbage. The mean live herbage biomass was 1630 lbs/ac with 93.9% invasive domesticated grasses, 2.2% native grasses, 2.2%

upland sedges, and 1.8% forbs. The rhizosphere biomass was reduced to 54.1 kg/m^3 (13.3% of potential weight) and the available mineral nitrogen was greatly reduced. After 6 years of twice-over rotation grazing management, the plant communities at site #1 had been restored about 41%. The aboveground vegetation biomass consisted of 35.6% standing dead and litter and 64.4% live herbage. The mean live herbage biomass was 2447 lbs/ac with 89.6% domesticated grasses, 3.5% native grasses, 2.0% upland sedges, and 4.9% forbs. The rhizosphere biomass had increased to 167.1 kg/m^3 (41.1% of potential weight) and the available mineral nitrogen had increased to 59.9 lbs/ac (Manske and Schneider 2012b) (table 1).

Restoration of degraded mesic mixed grass prairie ecosystems at site #2 dominated by Kentucky bluegrass was attempted by implementation of the twice-over rotation system. Before the grazing treatment started, the aboveground vegetation biomass consisted of 63.6% standing dead and litter and 36.4% live herbage. The mean live herbage biomass was 1645 lbs/ac with 64.8% invasive domesticated grasses, 3.3% native grasses, 22.9% upland sedges, and 9.0% forbs. The rhizosphere biomass had been reduced to 78.0 kg/m^3 (19.2% of potential weight) and the available mineral nitrogen was greatly reduced. After 6 years of twice-over rotation grazing management, the plant communities at site #2 had been restored about 53%. The aboveground vegetation biomass consisted of 39.3% standing dead and litter and 60.7% live herbage. The mean live herbage biomass was 2174 lbs/ac with 58.0% domesticated grasses, 26.1% native grasses, 11.3% upland sedges, and 4.6% forbs. The rhizosphere biomass had increased to 214.3 kg/m^3 (52.7% of potential weight) and the available mineral nitrogen had increased to 56.7 lbs/ac (Manske and Schneider 2012b) (table 1).

Degraded mixed grass prairie ecosystems that were subsequently invaded by introduced domesticated grasses have two additional major problems, increased shading and increased mulch biomass, that must be overcome by management in order to successfully restore the plant communities. Increased shading reduces rates of photosynthesis, reducing fixed carbohydrates supply, causing reduced growth rates of leaves and roots in understory native grasses. Increased mulch biomass reduces precipitation infiltration and early season soil temperatures causing reduced soil organism biomass and activity, slowed nutrient cycles, and decreased biogeochemical processes resulting in greatly reduced native plant density and in creating large open spaces for invasion of undesirable introduced domesticated grasses (Manske and Schneider 2012b).

The degraded mesic mixed grass prairie communities on sites #1 and #2 that were subsequently invaded by smooth bromegrass and Kentucky bluegrass, respectively, were not fully restored during the 6 years of management with the twice-over rotation system because the defoliation resistance mechanisms were not sufficiently activated as a result of insufficient quantities of fixed carbon and mineral nitrogen available to the understory native grass plants. The native grasses on sites #1 and #2 were inhibited by the severe deficiency of sunlight reaching the understory leaves caused by shading from accumulated domesticated grass live and standing dead leaves. The stocking rates were high enough only during 2 of the 6 years to remove sufficient quantities of domesticated grass live and standing dead leaves and reduce the detrimental shading effect. The low sunlight intensity caused reduced photosynthetic rates that resulted in a deficiency of available fixed carbon. A deficiency of available soil mineral nitrogen was caused by low rhizosphere biomass because of low carbon exudates released through the grass roots. The deficiency of sunlight attenuated by native grass leaves caused by shading must be corrected through grazing defoliation with relatively high stocking rates, at 85% to 100% of assessed levels, managed by the twice-over rotation strategy before degraded mixed grass prairie communities that were subsequently invaded by domesticated grasses can be fully restored back to functional native grass ecosystem (Manske and Schneider 2012b).

The amount of woody shrubs and trees growing on the northern mixed grass prairie prior to European settlement is not known quantitatively but appears to have been low. From the early aerial photographic record for parts of the Northern Plains, Smith (1988) reported that during the mid to late 1930's only about 5% of the upland landscape area was occupied by shrubs. Traditional management practices that have deferred the start of grazing until after mid July, grazed during early or late season (before June or after mid October), or grazed at heavy grass utilization stocking rates caused mixed grass prairie ecosystem degradation severe enough to end suppression of shrub growth and provided enough access to belowground resources to facilitate shrub invasion and expansion (Manske 2007a, 2011a). Long-term nongrazing has also caused severe degradation of mixed grass prairie ecosystems that has resulted in shrub invasion and expansion (Manske and Schneider 2012a). Antagonistic management practices have caused the abundant shrub cover greater than 5% on the regions upland landscapes.

The key to invasive woody shrub and tree and herbaceous plant control in grassland communities is to regain the competitive advantage of the grasses by restoration of the mechanisms and processes in the mixed grass prairie ecosystem that results from biologically effective partial defoliation by large grazing graminivores. Biological management of invaded shrubs with the twice-over rotation strategy improves the health and competitive abilities of the native grass plants and enhances the biogeochemical processes within the ecosystem (Manske 2011a, 2011b). With increasing competitiveness of native grasses for belowground resources of soil water and nutrients, the shrubs are detrimentally effected; the quantity of vegetative buds with activated meristematic tissue decreases, the growth rate of developing rhizome suckers decreases, and the mortality rate of young sucker stems increases. The effect of resource competition from healthy grasses causes the shrubs to decrease in density of rhizome and crown suckers, young stems, and total aerial stems, and causes a decrease in the canopy cover of shrub colonies. Unfortunately, this biological shrub control process is relatively slow and requires two to three decades to cause substantial shrub reductions.

Most deciduous shrubs and trees that grow in the Northern Plains, with the exception of big sagebrush, have the ability to reproduce vegetatively. Coniferous shrubs and trees do not reproduce vegetatively. Aerial stems of deciduous and coniferous shrubs are relatively easy to kill to the ground with a single treatment of prescribed burning, mechanical mowing, or chemical herbicide application. Successful deciduous shrub control management requires termination of the vegetative regenerative capabilities of the rhizomes and the stem bases on the crown.

Fire has been an environmental factor on mixed grass prairie as lightning-set fires and Indian-set fires. Spring burns result in great quantities of shrub sucker stems, and lost carbohydrate stores can be completely replenished by the new plant material in one growing season. August fires remove all or most of the top growth of shrubs and result in fewer sucker shoots the following year than spring burns. When the soil is not dry, prescribed burns during August cause the least damage to native cool season and warm season grasses and perennial forbs. The belowground rhizomes and crown stem bases are usually not damaged by fire because of the protection provided by soil. Some of the buds on the belowground parts develop into new aerial sucker stems. Prescribed burning alone will not remove deciduous shrubs that can reproduce vegetatively from the northern mixed grass prairie (Manske et al. 2006a, Manske 2007a, 2011a).

Mechanical mowing treatments can effectively reduce shrub stem densities if the stored nonstructural carbohydrate energy is depleted. Single annual mowing treatments do remove existing aerial stems, temporarily eliminating the competition for sunlight to the understory plants, but do not reduce shrub stem numbers because the regrowth of sucker stems can replenish the carbohydrate reserves during one growing season. Double mowing per growing season can reduce shrub stem numbers when the two mowing periods match shrub growth stages and cause carbohydrate depletion. The first mowing period should be conducted when the shrubs are at seasonal low carbohydrate reserve, which occurs between the end of rapid spring growth and the start of flowering; for many shrubs this first mow period occurs during the last week in May through the third week in June. The resulting new sucker shoot growth should continue to deplete carbohydrate reserves for nearly six weeks. At that time, these new suckers require mowing to reduce the leaf area that would replenish the carbohydrate stores. The second mowing period should be conducted when the new suckers have completed the rapid growth stage; for many shrubs this second mow period occurs during late July through August. This second mowing also causes a substantial amount of winter injury to the resulting late-season lateral bud sprouts on the stem bases. The mowing height in grazed pastures during both mowing periods should be about 8 to 9 inches above the ground. Stems cut short are rigid and can puncture the sole of the hoofs of cattle walking through mowed areas causing an injury open to infection. Double mowing treatments will need to be repeated two or more seasons until the carbohydrate reserves are fully depleted (Manske et al. 2006a).

Chemical management control of shrubs requires termination of the regenerative capabilities of the rhizomes and the crown stem bases by disabling the meristematic tissue. Foliage-active herbicides must enter the leaf tissue through the stomata openings or penetrate the outer cuticle layer, be absorbed through leaf tissue by diffusion, moved to the vascular system within the leaf, and be translocated from the leaves downward through the phloem vascular system to the metabolically active sites of the crowns and rhizomes. During rapid stem elongation, nonstructural carbohydrates move from the storage sites in the rhizomes and the crowns upward through the phloem vascular system to the active growing points of the stem preventing downward movement of herbicides. As leaf area increases and carbohydrate production by photosynthesis exceeds the demands for growth, the surplus carbohydrates are moved downward through the phloem for storage in the rhizomes and crowns (Coyne et al. 1995); downward translocation of herbicides could occur at that time if the herbicides were in the leaf tissue. However, as leaves mature, they develop a thick cuticle layer and dense cell walls reducing herbicide penetration and absorption. Most shrubs have a brief vulnerable stage when the herbicide plus surfactant penetration into leaf tissue is decreasing and herbicide translocation downward is increasing. For many shrubs this short period occurs from about 10 June until 20 June.

Soil-active herbicides, like tebuthiuron (Spike 20P), have a relatively wide window of opportunity for treatment and require only that application be ahead of a rainy period. The herbicide moves into the roots anytime the roots are absorbing water. Movement upward in the xylem vascular system is not as complex as movement within the phloem system. Plants have few resistance mechanisms to restrict activity of soil-applied herbicides. Usually low rates are quite effective (Manske et al. 2006a, Manske 2006b).

Restoration of degraded mixed grass prairie ecosystems that have been subsequently invaded by woody shrubs requires regaining the competitive advantage of fully activated physiological and biogeochemical processes of healthy native grass plants through biologically effective management of grazing graminivores and requires termination of the vegetative regenerative capabilities of the shrubs rhizomes and stem bases through combinations of biological, prescribed burning, mechanical mowing, and chemical herbicide management practices.

Recapitulation

Mixed grass prairie ecosystems are complex and consist of numerous biotic and abiotic components that function together through three primary processes; the defoliation resistance mechanisms, the ecosystem biogeochemical processes; and the plant resource uptake processes. When these three primary processes do not function at potential level, the ecosystem does not function at potential level. Partial defoliation by grazing graminivores is required to trigger activation of the primary processes and the quantity of available soil mineral nitrogen and the quantity of available fixed carbon affect the level at which the primary processes function. Fully functioning processes require mineral nitrogen to be available at 100 lbs/ac or greater and require the quantity of carbon fixed through photosynthesis from 75% to 67% of the leaf area of grass lead tillers prior to peak live herbage biomass and from 50% of the leaf area post peak biomass.

The primary processes function at less than potential levels when soil mineral nitrogen and fixed carbon are available at quantities less than the threshold amounts and the processes are not activated when grazing graminivores do not remove 25% to 33% of lead tiller leaf area during vegetative growth stages between the 3.5 new leaf stage and the flower stage. When the defoliation resistance mechanisms, the biogeochemical processes, and the resource uptake processes function at degraded levels, the mixed grass prairie ecosystems are degraded to the levels at which the primary processes are functioning.

A reduction in the condition of the aboveground vegetation is a visable symptom that the primary processes are functioning at degraded levels. The symptom of descending quality of the vegetation from desirable native grasses, to less desirable domesticated grasses, to undesirable shrubs indicates the increasing severity in the deterioration of the primary ecosystem processes. The symptoms of descending changes in the vegetation lag behind the descending changes in the functionality of the primary processes.

Restoration of degraded mixed grass prairie ecosystems requires returning the three primary ecosystem processes back to functioning at potential levels. The rhizosphere organism biomass must be improved initially to increase mineralization of nitrogen and other essential elements. Rhizosphere organisms are limited by access to energy in the form of short carbon chains. Exudation of short carbon chain energy can be released from the grass lead tillers through the roots into the rhizosphere by removal of 25% to 33% of the aboveground leaf biomass by large grazing graminivores when the lead tillers are between the 3.5 new leaf stage and the flower stage. As a result of this successful initial recovery of the biogeochemical processes, the amounts of available mineral nitrogen, essential elements, fixed carbon, and soil water start increasing from deficient quantities towards functional quantities. With the increasing component resources, native grass plants are able to synthesize increasing quantities of carbohydrates, proteins, and nucleic acids. Activation of the defoliation resistance mechanisms provides important biological and physiological processes permitting native grasses to use the vital organic compounds in increasing quantities for the production of herbage biomass and basal cover. With implementation of the belowground resource uptake of soil water, mineral nitrogen, and other essential elements, the native grasses become more competitive. The symptoms of improving changes in the vegetation lag behind the improving changes in the functionality of the primary processes.

Restoration of degraded mixed grass prairie ecosystems that were subsequently invaded by introduced domesticated grasses requires reduction of two additional problems, the increased shading from domesticated grass live and standing dead leaves and the increased mulch biomass. Both problems are corrected by stocking rates at 85% to 100% of assessed levels. The high stocking rates removes sufficient quantities of domesticated grass leaf material to reduce the shading effect of low sunlight intensity and the weight of the greater number of animals pushes the mulch biomass into contact with the soil where microbial decomposition can take place.

Restoration of degraded mixed grass prairie ecosystems that were subsequently invaded by woody shrubs requires termination of the vegetative regenerative capabilities of the shrubs rhizomes and stem bases through combinations of biological, prescribed burning, mechanical mowing, and chemical herbicide management practices.

Restoration of degraded mixed grass prairie ecosystems requires annual partial defoliation by grazing graminivores managed by the biologically effective twice-over rotation strategy that coordinates defoliation events with grass phenological growth stages. The twice-over strategy activates the defoliation resistance mechanisms, the biogeochemical processes, and the resource uptake processes, and then maintains their functionality at potential levels. The twice-over strategy also meets the biological requirements of the grass plants and the rhizosphere organisms, and meets the nutritional requirements of the grazing animals. Biologically effective management of restored mixed grass prairie ecosystems sustains healthy renewable natural resources that simultaneously provide greater forage for livestock, better habitat for wildlife, more aesthetic prairie ecosystems for recreation and sightseeing, and increased food and fiber for people.

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Table 1. Mineral nitrogen and rhizosphere volume or biomass for degraded and restored mixed grass prairie ecosystems.

Management Treatment		Mineral Nitrogen lbs/ac	Rhizosphere Volume ft^3/ac	Rhizosphere Biomass kg/m^3
		Degradation from Traditional Grazing Practices		
4.5 m Seasonlong	20 yr	76.7	67.6	
6.0 m Seasonlong	20 yr	61.6	49.8	
7.0 m Seasonlong	75 yr	42.4		154.7
Deferred Grazed	50 yr	31.2		-
		Degradation from Nondefoliation		
Nongrazed Site #1	13 yr	-		54.1
Nongrazed Site #2	13 yr	-		78.0
Nongrazed Long-term	75 yr	39.5		127.2
		Restoration from Biologically Effective Defoliation		
Restored Ecosystem	20 yr	177.8	227.1	406.4
Restored Site #1	6 yr	59.9		167.1
Restored Site #2	6 yr	56.7		214.3

Literature Cited

Anderson, R.V., D.C. Coleman, C.V. Cole, and E.T. Elliott. 1981. Effect of nematodes Acrobeloides sp. and Mesodiplogaster lheritieri on substrate utilization and nitrogen and phosphorus mineralization. Ecology 62:549-555

Bird, S.B., J.E. Herrick, M.M. Wander, and S.F. Wright. 2002. Spatial heterogeneity of aggregate stability and soil carbon in semi-arid rangeland. Environmental Pollution 116:445-455.

Briske, D.D. 1991. Developmental morphology and physiology of grasses. p. 85-108. in R.K. Heitschmidt and J.W. Stuth (eds.). Grazing management: an ecological perspective. Timber Press, Portland, OR.

Briske, D.D., and J.H. Richards. 1994. Physiological responses of individual plants to grazing: current status and ecological significance. p. 147-176. in M. Vavra, W.A. Laycock, and R.D. Pieper (eds.). Ecological implications of livestock herbivory in the west. Society for Range Management, Denver, CO.

Briske, D.D., and J.H. Richards. 1995. Plant response to defoliation: a physiological, morphological, and demographic evaluation. p. 635-710. in D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Burrows, R.L., and F.L. Pfleger. 2002. Arbuscular mycorrhizal fungi respond to increasing plant diversity. Canadian Journal of Botany 80:120-130.

Coleman, D.C., C.P.P. Reid, and C.V. Cole. 1983. Biological strategies of nutrient cycling in soil ecosystems. Advances in Ecological Research 13:1-55.

Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995. Carbon and nitrogen dynamics in range plants. p. 59-167. in D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Crider, F.J. 1955. Root-growth stoppage resulting from defoliation of grass. USDA Technical Bulletin 1102.

Curl, E.A., and B. Truelove. 1986. The rhizosphere. Springer-Verlag, New York, NY.

Daubenmire, R.F. 1974. Plants and Environment: A textbook of plant autecology. 3rd ed. John Wiley & Sons. New York, NY.

Driver, J.D., W.E. Holben, and M.C. Rillig. 2005. Characterization of glomalin as a hyphal wall component of arbuscular mycorrhizal fungi. Soil Biology and Biochemistry 37:101-106.

Grant, S.A., G.T. Barthram, L. Torvell, J. King, and H.K. Smith. 1983. Sward management, lamina turnover and tiller population density in continuously stocked *Lolium perenne*-dominated swards. Grass and Forage Science 38:333-344.

Hamilton, III, E.W., and D.A. Frank. 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82:2397-2402.

Heady, H.F. 1975. Rangeland Management. McGraw-Hill Book Co. New York, NY.

Humphrey, R.R. 1962. Range Ecology. The Ronald Press Co. New York, NY.

Ingham, R.E., J.A. Trofymow, E.R. Ingham, and D.C. Coleman. 1985. Interactions of bacteria, fungi, and the nemotode grazers: effects of nutrient cycling and plant growth. Ecological Monographs 55:119-140.

Kirsch, L.M., and A.D. Kruse. 1972. Prairie fires and wildlife. Proceedings of Tall Timbers Fire Ecology Conference. 12:289-303.

Klein, D.A., B.A. Frederick, M. Biondini, and M.J. Trlica. 1988. Rhizosphere microorganism effects on soluble amino acids, sugars, and organic acids in the root zone of Agropyron cristatum, A. smithii, and Bouteloua gracilis. Plant and Soil 110:19-25.

Kochy, M., and S.D. Wilson. 2000. Competitive effects of shrubs and grasses in prairie. Oikos 91:385-395.

Kochy, M. 1999. Grass-tree interactions in western Canada. Ph.D. Dissertation. University of Regina. Regina, Saskatchewan, Canada.

Langer, R.H.M. 1972. How grasses grow. Edward Arnold, London, Great Britain.

Li, X., and S.D. Wilson. 1998. Facilitation among woody plants establishing in an old field. Ecology 79:2694-2705.

Manske, L.L. 1999. Can native prairie be sustained under livestock grazing? p. 99-108. in J. Thorpe, T.A. Steeves, and M. Gollop (eds.). Proceedings of the Fifth Prairie Conservation and Endangered Species Conference. Provincial Museum of Alberta. Natural History Occasional Paper No. 24. Edmonton, Alberta, Canada.

Manske, L.L. 2000. Management of Northern Great Plains prairie based on biological requirements of the plants. NDSU Dickinson Research Extension Center. Range Science Report DREC 00-1028. Dickinson, ND. 12p.

Manske, L.L., S.A., Schneider, and A.M. Kraus. 2006a. Management of western snowberry aka wolfberry and buckbrush. NDSU Dickinson Research Extension Center. Rangeland Research Extension Program 4009. Dickinson, ND. 107p.

Manske, L.L. 2006b. Chemical management of silver sagebrush. NDSU Dickinson Research Extension Center. Range Research Report DREC 06-1065. Dickinson, ND. 38 p.

Manske, L.L. 2007a. Effects on vegetation, endomycorrhizal fungi, and soil mineral nitrogen from prescribed burning treatments repeated every-other-year in mixed grass prairie invaded by western snowberry. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 07-3044. Dickinson, ND. 19p.

Manske, L.L. 2007b. Restoration of degraded prairie ecosystems. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 07-3045. Dickinson, ND. 6p.

Manske, L.L. 2009. Grass plant responses to defoliation. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1074. Dickinson, ND. 47p.

Manske, L.L. 2010a. Leaf stage development of western wheatgrass tillers. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1075. Dickinson, ND. 48p.

Manske, L.L. 2010b. Evaluation of the defoliation resistance mechanisms influence on vegetative tiller initiation and tiller density. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1076. Dickinson, ND. 13p.

Manske, L.L., S. Schneider, J.A. Urban, and J.J. Kubik. 2010. Plant water stress frequency and periodicity in western North Dakota. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1077. Dickinson, ND. 11p.

Manske, L.L. 2011a. Grazing and burning treatment effects on soil mineral nitrogen and rhizosphere volume. NDSU Dickinson Research Extension Center. Range Research Report DREC 11-1066c. Dickinson, ND. 15p.

Manske, L.L. 2011b. Biology of defoliation by grazing. NDSU Dickinson Research Extension Center. Range Management Report DREC 11-1067b. Dickinson, ND. 25p.

Manske, L.L., and S.A. Schneider. 2012a. Effects from long-term nongrazing after 75 years. NDSU Dickinson Research Extension Center. Rangeland Research Outreach Program 4016. Dickinson, ND.

Manske, L.L., and S.A. Schneider. 2012b. Evaluation of biological restoration management of degraded native mixed grass prairie. NDSU Dickinson Research Extension Center. Rangeland Research Outreach Program 4017. Dickinson, ND.

McNughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist 113:691-703.

McNaughton, S.J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329-336.

Mueller, R.J., and J.H. Richards. 1986. Morphological analysis of tillering in Agropyron spicatum and Agropyron desertorum. Annuals of Botany 58:911-921.

Murphy, J.S., and D.D. Briske. 1992. Regulation of tillering by apical dominance: chronology, interpretive value, and current perspectives. Journal of Range Management 45:419-429.

Peltzer, D.A., and M. Kochy. 2001. Competitive effects of grasses and woody plants in mixed grass prairie. Journal of Ecology 89:519-527.

Richards, J.H., and M.M. Caldwell. 1985. Soluble carbohydrates, concurrent photosynthesis, and efficiency in regrowth following defoliation: a field study with *Agropyron* species. Journal of Applied Ecology 22:907-920.

Richards, J.H., R.J. Mueller, and J.J. Mott. 1988. Tillering in tussock grasses in relation to defoliation and apical bud removal. Annals of Botany 62:173-179.

Rillig, M.C., S.F. Wright, and V.T. Eviner. 2002. The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. Plant and Soil 238:325-333.

Smith, K.A. 1988. Lostwood National Wildlife Refuge station plan. US Fish and Wildlife Service.

Stoddart, L.A., A.D. Smith, and T.W. Box. 1975. Range Management. 3rd ed.. McGraw-Hill Book Co. New York, NY.

Weaver, J.E. 1954. North American Prairie. Johnsen Publishing Co. Lincoln, NE.

Whipps, J.M. 1990. Carbon economy. p. 59-97. in J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

Whitman, W.C. 1974. Influence of grazing on the microclimate of mixed grass prairie. p. 207-218. *in* Plant Morphogenesis as the basis for scientific management of range resources. USDA Miscellaneous Publication 1271.

Wight, J.R., and A.L. Black. 1972. Energy fixation and precipitation use efficiency in a fertilized rangeland ecosystem of the Northern Great Plains. Journal of Range Management 25:376-380.

Wight, J.R., and A.L. Black. 1979. Range fertilization: plant response and water use. Journal of Range Management 32:345-349.

Wright, H.A., and A.W. Bailey. 1982. Fire Ecology: United States and southern Canada. John Wiley & Sons. New York, NY.

Perpetually Sustainable Grazingland Ecosystems

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Grassland ecosystems are open systems with biological, chemical, and atmospheric pathways that transfer essential elements into, inputs (gains), and out of, outputs (losses), the ecosystem. Grazingland ecosystems that have greater output than input of essential elements are deteriorating and not sustainable. Ecosystems that have greater natural input than output of essential elements are healthy and sustainable (Manske 2012).

The major essential elements of carbon, hydrogen, nitrogen, and oxygen have separate but closely linked biogeochemical cycles that transform the elements between organic forms and inorganic forms. Healthy ecosystems retain most of the essential elements as immobilized organic compounds, with a portion contained in living organisms and about 4 to 5 times that amount as detritus. Soil microorganisms cycle a portion of the essential elements from organic detritus into inorganic forms each growing season. The quantity of essential elements mineralized by soil microorganisms determines the quantity of annual biomass production (Manske 2009, 2011a).

Soil organisms and plants use the essential elements in the inorganic form to synthesize vital organic compounds of carbohydrates, proteins, and nucleic acids. Grass plants produce double the quantity of leaf biomass than needed for normal plant growth (Crider 1955, Coyne et al. 1995). All of the aboveground herbage biomass produced by perennial grasses in a growing season represents about 33% of the total biomass produced. About 67% of the annual perennial grass biomass is produced belowground. About 50% of the aboveground biomass is expendable by the plant. About half of the expendable leaf material is removed as senescent leaves that are broken from the plant and fall to the ground, or as leaf material consumed by insects and wildlife. About half of the expendable leaf material, or 25% of the aboveground biomass, is consumed by grazing livestock (Manske 2012).

Perennial grass leaf material consists of digestible nutrients and nondigestible structural components. About 15% of the nutrients contained in the consumed leaf material is extracted by stocker heifers and steers and retained for growth. About 30% of the nutrients contained in the consumed leaf material is extracted by lactating cows, with a portion retained by the cow for production, and the remainder of the extracted nutrients passed on to her calf for growth (Russelle 1992, Gibson 2009).

All of the nondigestible dry matter and most of the nutrients consumed by grazing livestock are deposited on the ground as manure in a couple of days. Most of the nutrients consumed and used by livestock for maintenance are returned to the ecosystem in the feces and urine. None of the herbage biomass dry matter produced during a growing season is removed by livestock from the grazingland ecosystem. All of the essential elements contained in the belowground biomass and contained in the nonconsumed aboveground biomass stay in the ecosystem. Nearly all of the essential elements used in the annual production of herbage biomass and soil organism biomass are retained and recycled in the ecosystem.

Some essential elements are lost or removed from the ecosystem as output. If the grassland ecosystem is burned, almost all of the essential elements in the aboveground herbage are volatilized, and if the soil is dry, some of the belowground essential elements are also lost (Russelle 1992). The metabolic process of respiration in soil organisms, plants, and animals results in a loss of some essential elements as carbon dioxide, water vapor, and heat energy. Some essential elements are removed from the ecosystem as weight biomass produced by insects and wildlife. The essential elements transferred from grass plants to grazing animals and used for animal growth are removed from the ecosystem (Gibson 2009).

The small proportion of the ecosystem essential elements that are lost or removed annually need to be replenished by capturing input essential elements through ecosystem processes. These ecological processes consist of energy (TDN) flow (table 1), nitrogen flow (table 2), and decomposition of organic matter (table 3). Atmospheric carbon dioxide is the ecosystem input for carbon. Precipitation of water is the ecosystem input for hydrogen. Wet deposition of nitrogen oxides following lightning discharges is the ecosystem input for nitrogen. Carbon dioxide, water, and nitrogen oxides are the ecosystem input for oxygen. Radiant light from the sun is the ecosystem input for energy (Manske 2011b). The input sources of essential elements are not part of the ecosystem supply until the ecosystem processes capture the input essential elements (Manske 2012).

Ecosystem processes are inhibited from functioning at potential levels by antagonistic management practices preventing capture of essential elements from input sources at quantities adequate to replenish annually lost or removed elements. The resulting increasing deficiencies of essential elements cause decreasing production and ecosystem degradation (Manske 2012).

Perpetually sustainable grazingland ecosystems can be achievable with implementation of biologically effective management that activates all ecosystem biogeochemical processes and all grass plant physiological processes to function at potential levels. When these processes function above threshold levels, capture and replenishment of input essential elements occurs at greater quantities than the amount of output essential elements (Manske 2012).

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Table 1. Energy (TDN) flow.

Grazingland ecosystem energy flow includes three biogeochemical cycles: the carbon cycle, the hydrogen cycle, and the oxygen cycle.

Photosynthesis is the process that captures energy.
$CO_2 + 2H_20$ + sunlight energy + green plants $\Rightarrow CH_20 + 0_2$

Respiration is the process that releases energy.
$C_6H_{12}0_6 + 60_2 \Rightarrow 6C0_2 + 6H_20$ + heat energy

Table 2. Nitrogen flow.

Grazingland ecosystem nitrogen flow is primarily the nitrogen cycle and includes three other biogeochemical cycles: the oxygen cycle, the carbon cycle, and the hydrogen cycle.

Wet Deposition is the process that changes nitrogen from atmospheric forms to edaphic forms.
$N_2 + 0_2$ + lightning discharge $\Rightarrow N0 + N_20$ at 5 to 6 lbs/ac/yr = 3 to 8 tons/ac

Immobilization is the process that changes nitrogen from inorganic forms to organic forms (nucleic acids and crude proteins).
$NH_4 + N0_3$ + grass plants + soil organisms $\Rightarrow$ nucleic acids + amino acids $\Rightarrow$ crude protein + organic compounds

Mineralization is the process that changes nitrogen from organic forms to inorganic forms (mineral nitrogen).
Organic matter + saprophytes $\Rightarrow NH_3 + C0_2$
$NH_3 + H \Rightarrow NH_4$
$2NH_4 + 30_2$ + Nitrosomonas $\Rightarrow 2N0_2 + 2H_20 + 4H$ + energy
$2N0_2 + 0_2$ + Nitrobacter $\Rightarrow 2N0_3$ + energy

Table 3. Decomposition of organic matter.

Grazingland ecosystem organic matter decomposition includes all of the biogeochemical cycles.

Decomposition is the process that changes complex organic matter into compounds and then into the elemental forms.

Dead organic matter + saprophytes $\Rightarrow$ 150% microbe biomass + $C0_2 + H_20$ + minerals

Compound Composition		Elemental Composition	
Carbohydrates	60%	Carbon	44%
Sugars and Starches	1-5%	Oxygen	40%
Hemicelluloses	10-30%	Hydrogen	8%
Cellulose	20-50%	Minerals	8%
Lignins	10-30%		
Fats, Waxes, Tannins	1-8%		
Protein	1-15%		

Literature Cited

Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995. Carbon and nitrogen dynamics in range plants. p. 59-167. in D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Crider, F.J. 1955. Root-growth stoppage resulting from defoliation of grass. USDA Technical Bulletin 1102.

Gibson, D.J. 2009. Grasses and grassland ecology. Oxford University Press Inc., New York, NY. 305p.

Manske, L.L. 2009. Enhancement of the nitrogen cycle improves native rangeland. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 09-3054. Dickinson, ND. 6p.

Manske, L.L. 2011a. Soil mineral nitrogen increased above the threshold quantity of 100 pounds per acre in rangeland ecosystems. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 11-3056. Dickinson, ND. 8p.

Manske, L.L. 2011b. Biology of defoliation by grazing. NDSU Dickinson Research Extension Center. Range Management Report DREC 11-1067b. Dickinson, ND. 25p.

Manske, L.L. 2012. Degradation and biological restoration of mixed grass prairie ecosystems. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 12-3058. Dickinson, ND. 16p.

Russelle, M.P. 1992. Nitrogen cycling in pastures and range. Journal of Production Agriculture. 5:13-23.

Initial Restoration Changes of Degraded Rangeland with the Twice-over Rotation Grazing Strategy

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Biogeochemical processes are the processes that renew nutrient flow activities in ecosystem soils of renewable natural resources. The biogeochemical processes of rangeland natural resources managed with traditional management practices are impeded from functioning at potential levels. Traditional practices that: 1. start grazing too early, before the 3.5 new leaf stage; 2. remove greater than 25% to 33% of green leaf biomass before the flower stage; 3. start grazing too late, after the flower stage; 4. remove greater than 50% of green leaf biomass after peak aboveground herbage biomass produced in late July; 5. continue grazing carryover tillers, after mid October; or 6. "rest" vegetation with nondefoliation during parts or entire growing seasons to increase seed production; are detrimental to the ecosystem biogeochemical processes and are antagonistic to the native plants and soil organisms causing degradation of rangeland renewable natural resources.

Traditional management practices also diminish the compensatory physiological processes, the vegetative reproduction mechanisms, and the rhizosphere organism population (Manske 2011). Decreases in vegetative reproduction by tillering and reductions of compensatory physiological processes prevent grass tillers from replacing a sufficient proportion of the leaf area removed by partial defoliation. Low leaf surface area reduces the quantity of carbon fixed by photosynthesis. Decreases in rhizosphere organism biomass and activity result in decreased biogeochemical processes of the nitrogen cycle causing reductions in the quantity of organic nitrogen converted into mineral nitrogen (Manske 2007). Decreases in the availability of the quantity of fixed carbon and the quantity of mineral nitrogen in an ecosystem degrade grassland plant communities by causing reductions in grass herbage biomass production and native plant density, creating larger and more numerous open spaces between grass plants. These open spaces in the plant communities provide ideal habitat for growth of opportunistic "weedy" plant species that are not dependent on the nitrogen converted by rhizosphere organisms (Manske 2011). Opportunistic grasses and forbs are not highly competitive and do not increase into plant communities unless openings are created by management caused reductions in native grass densities. Degraded grassland ecosystems have an increasing composition of opportunistic introduced grasses, early succession and weedy forbs, and shrubs (Manske 2007).

This project will describe and evaluate development of biological restoration of degraded rangeland resources through implementation of biological effective grazing management. Quantitative annual changes of aboveground herbage biomass, plant species basal cover, forb density, rhizosphere biomass, and available soil mineral nitrogen will document progress of rangeland ecosystem restoration.

Study Area

Restoration research was conducted during 2006 to 2011 on 1,988 acres (804.5 hectares) of degraded native rangeland located about 2 miles (3.22 kilometers) east of the town of Richardton, eastern Stark County in western North Dakota, between 47° 00' and 46° 50' north latitude and between 102° 20' and 102° 10' west longitude.

The untilled rangelands with native plant ecosystems became severely degraded by traditional management practices that were antagonistic to native plant and soil rhizosphere organism biological requirements and to ecosystem biogeochemical processes causing great decreases in the native plant density and herbage biomass. The degraded rangelands subsequently became invaded with undesirable introduced cool season domesticated grasses, primarily kentucky bluegrass with smaller areas of smooth bromegrass and crested wheatgrass, that caused additional problems of shading and increased mulch biomass.

Regional Climatic Factors

The western North Dakota region near Richardton has cold winters and hot summers typical of continental climates. Mean annual temperature is

43.0° F (6.1° C). January is the coldest month, with a mean temperature of 13.5° F (-10.3° C). July and August are the warmest months, with mean temperatures of 70.0° F (21.1° C) and 68.9° F (20.5° C), respectively. Long-term (1971-2000) mean annual precipitation is 17.78 inches (451.61 mm). The precipitation during the perennial plant growing season (April through October) is 14.79 inches (375.67 mm) and is 83.2% of the annual precipitation. June has the greatest monthly precipitation, at 3.39 inches (86.11 mm). The precipitation received during the three month period of May, June, and July is 8.15 inches (207.01 mm) and is 45.8% of the annual precipitation.

Water stress develops in perennial plants during water deficiency periods when the amount of rainfall is less than evapotranspiration demand. Water deficiency months were identified from historical temperature and precipitation data by the ombrothermic diagram technique (Emberger et al. 1963). The long-term (1971-2000) ombrothermic diagram shows near water deficiency conditions during August, September, and October, and favorable water relations during April, May, June, and July. Reoccurrence of water deficiency conditions during April, May, June, and July is 16.9%, 13.6%, 10.2%, and 38.1%, respectively, and during August, September, and October water deficiency reoccurs 52.5%, 50.0%, and 46.6% of the years, respectively. Long-term occurrence of water deficiency conditions is 32.7% of the growing season months, for a mean of 2.0 water deficient months per growing season (Manske et al. 2010).

Mean growing season precipitation during the six years of the study was 12.31 inches (83.23% of LTM). During the first three years, growing season precipitation was 9.42, 10.75, and 11.45 inches, respectively, with a mean of 10.54 inches (71.26% of LTM). During the last three years, growing season precipitation was 11.63, 13.43, and 17.15 inches, respectively, with a mean of 14.07 inches (95.13% of LTM) (table 1).

Grazing Management

Restoration of native mixed grass prairie ecosystem biogeochemical processes and plant species composition on degraded rangeland requires implementation of a biologically effective grazing management strategy that activates the defoliation resistance mechanisms and ecosystem biogeochemical processes (Manske 2011). These mechanisms are: compensatory internal physiological processes, internal vegetative reproduction of secondary tillers from axillary buds, and external symbiotic rhizosphere organism activity (McNaughton 1979, 1983; Coleman et al. 1983; Ingham et al. 1985; Mueller and Richards 1986; Richards et al. 1988; Briske 1991; Murphy and Briske 1992; Briske and Richards 1994, 1995; Manske 1999, 2011). The defoliation resistance mechanisms accelerate growth rates of replacement roots, leaves, and shoots, increase photosynthetic capacity of remaining mature leaves, increase allocation of carbon and nitrogen, increase secondary tiller development from axillary buds, and increase conversion of soil organic nitrogen into plant usable mineral nitrogen (Manske 2011).

The twice-over rotation grazing management strategy was the biologically effective management practice implemented to restore the degraded mixed grass prairie biogeochemical processes and native plant communities. During 2006 to 2011, three grassland pastures were grazed from early June until mid October, with each pasture grazed for two periods. A fourth pasture was not grazed and was used as a control. Each of the three pastures in the rotation was grazed for 14 to 16 days during the first period, the 45 day interval from 1 June to 15 July, during which the defoliation resistance mechanisms can be activated by partial defoliation by grazing (Manske 1999, 2011). The length of the first period on each pasture was the same percentage of 45 days as the percentage of the total season's grazeable forage contributed by each pasture (Manske 2000). During the second period, the 90 day interval from mid July to mid October, each pasture was grazed for double the number of days that it was grazed during the first period. The first pasture grazed in the rotation sequence was the last pasture grazed the previous year.

The stocking rate on the study area was assessed using recently updated ecological site maps and determined that a total of 789.90 AUM's of forage was available on the 1,519 acres of the three grazed pastures. With a grazing season of 4.5 months from early June to mid October, 175 AU's with a total herd weight of 175,533 pounds could graze at a stocking rate of 1.92 ac/AUM. The intended stocking rates were to graze at 75%, 85%, and 95% of the assessed stocking rate during years 1, 2, and 3, respectively, and thereafter to graze at slightly less than 100% of the assessed stocking rate for the duration of the study. The actual stocking rates used during the study were a little different than the intended stocking rates. Heavy weight livestock (1450 lbs mean weight) grazed at 72.3%, 82.6%, and 107.5% of the assessed stocking rate during years 1, 2, and 3, respectively. Medium weight livestock (900 lbs mean weight) grazed at 79.8% and 87.4% of the assessed stocking rate during years 4 and 5, respectively. Light weight livestock (650 lbs mean weight) grazed at 37.8% of the assessed stocking rate during year 6.

The twice-over rotation grazing management strategy coordinates defoliation by grazing with grass phenological growth stages which improves plant health and activates biological and ecological processes within grass plants and the ecosystem so that beneficial changes to plant growth, rhizosphere organisms, and biogeochemical cycles in the ecosystem result (Manske 2000). During the first grazing period, grass lead tillers are between the three and a half new leaf stage and the flower (anthesis) stage; these are the vegetative stages of tiller development at which partial defoliation by grazing produces beneficial effects by activating the defoliation resistance mechanisms that increase compensatory growth rates, increase tillering from axillary buds, and enhance activity of rhizosphere organisms. Increased compensatory growth rates replace leaf and stem material at greater quantities than that removed by grazing substantially increasing the amounts of herbage biomass production. Increased vegetative reproduction by tillering contributes to the development of greater plant basal cover and to the production of greater grass herbage weight. Increased activity of the soil organisms in the rhizosphere supplies the plant with greater quantities of essential nutrients, primarily mineral nitrogen, to support additional growth (Manske 2000, 2011). Removal of livestock from native rangeland pastures in mid October, towards the end of the perennial grass growing season, allows grass plants to store carbohydrates and nutrients needed to maintain plant processes over the winter that will retain the fall vegetative tiller growth and the other carryover tillers which become next season's tillers (Manske 2003, 2011). The twice-over grazing strategy ensures healthy plants in the spring and greater herbage production during the next growing season (Manske 2000, 2011).

Renewable natural resources are complex ecosystems with several trophic layers of living organisms that have biological requirements, and with numerous nonliving components that have characteristics that are transformable between organic and inorganic forms. Management of renewable natural resources needs to meet all the requirements of the living and nonliving components of the ecosystem for the purpose of improving the biogeochemical processes and maintaining production at potential sustainable levels.

Continued ecosystem production at potential sustainable levels of rangeland and grassland renewable natural resources requires that management meets the biological requirements of the plants and soil organisms. The ecosystem biogeochemical processes and the organism physiological mechanisms that provide the biological requirements for grassland plants and rhizosphere organisms must be activated annually with partial defoliation by large graminivores during vegetative growth stages. Grazing animals are a necessity for full functionality of grassland plants and rhizosphere organisms.

Performance of the defoliation resistance mechanisms and biogeochemical processes ensure healthy productive native grass plants, active rhizosphere organisms, and fully functioning mixed grass prairie ecosystems. Activation of the mechanisms and processes result in increased herbage biomass production, increased plant density (basal cover), increased available forage nutrients, increased soil aggregation, improved soil quality, increased soil water holding capacity, increased resistance to drought conditions, improved wildlife habitat, improved grassland aesthetics, and improved grassland ecosystem quality (Manske 2011).

Procedures

The effects from a biologically effective grazing management strategy in the restoration of native mixed grass prairie ecosystem biogeochemical processes and grassland plant species composition on degraded untilled rangeland were evaluated in four pastures on silty ecological sites with permanent sample plots organized in a paired-plot design. A 16' X 32' (4.88 m X 9.75 m) stock panel exclosure prevented livestock access to an ungrazed plot. A grazed plot on an adjacent area of equal size was accessible by livestock. Ungrazed and grazed plots were established at each reference site for nondestructive data collection. An additional area of similar size accessible by livestock was established at each reference site for destructive data collection. Ecosystem changes in aboveground herbage biomass, plant species basal cover, forb density, and rhizosphere biomass were evaluated with data collected from late May through mid October during six growing seasons, 2006 to 2011. The plant basal cover and forb density data were collected along permanent transect lines established at each nondestructive sample site both inside (ungrazed) and outside (grazed) each exclosure. The major transect lines were parallel to each other on opposite sides of the exclosure fence. The minor transect lines were perpendicular to the major transect lines and were parallel to each other.

Aboveground herbage biomass was collected by the standard clipping method (Cook and Stubbendieck 1986) at each pasture rotation date, with seven clip periods per year. The herbage material from five 0.25 m^2 quadrats (frames) at each destructive sample site outside (grazed) each exclosure was hand clipped to ground level and sorted in the field by biotype categories: domesticated grasses, cool season grasses, warm season grasses, upland sedges, forbs, standing dead, and litter. 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. Herbage biomass in pounds per acre for each category were determined from the clipping data. Mean monthly herbage biomass for each category were determined for each growing season. Relative composition of herbage biomass biotype categories were determined.

Plant species basal cover was determined by the ten-pin point frame method (Cook and Stubbendieck 1986), with 2000 points collected along permanent transect lines during peak growth between mid July and mid August. Basal cover plant species data were sorted into biotype categories: domesticated grasses, cool season grasses, warm season grasses, upland sedges, forbs, and litter. Percent basal cover and relative composition of basal cover for the biotype categories were determined from the ten-pin point frame data.

Density of forbs were determined by counting individual stems of each plant species rooted inside twenty five 0.1 m^2 quadrats placed along permanent transect lines between mid July and mid August. Forb species were categorized as: late succession, mid succession, and early succession forbs. Density per 0.1 m^2 and relative composition of forb categories were determined from the forb density data.

Rhizosphere biomass was collected at each destructive sample site outside (grazed) each exclosure by three replicated soil cores 3 inches (7.6 cm) in diameter and 4 inches (10.2 cm) in depth during 3 grazing season periods: pregrazing (May), first rotation (July), and second rotation (October) using a humane soil beastie catcher (Manske and Urban 2012). The fresh rhizosphere material, which included the rhizosphere organisms, the active plant roots, and the adhered soil particles, was separated from matrix soil by meticulous excavation with fine hand tools. Both wet and dry rhizosphere weights were collected. Rhizosphere biomass per volume of soil was determined from the soil core rhizosphere weight data and reported as kilograms per cubic meter.

Soil mineral nitrogen, nitrate and ammonium, was sampled towards the end of the sixth grazing season from both inside (ungrazed) and outside (grazed) each exclosure by three replicated soil cores with 6 inch (15.2 cm) increments to a 12 inch (30.5 cm) depth collected using a Veihmeyer soil tube with 1 inch (2.5 cm) diameter. Soil cores were placed on ice immediately and were frozen within 2 to 3 hours of collection. Analysis of soil core samples for available mineral nitrogen (NO_3 and NH_4) was conducted by the North Dakota State University Soil Testing Laboratory. Total available mineral nitrogen at a one foot depth was determined from the soil core data and reported as pounds per acre.

Interpretation of treatment effects on plant community characteristics assumes only minor differences in the vegetation of the grazed area and ungrazed area at the time of exclosure construction on each reference site. A standard t-test was used to analyze differences among means (Mosteller and Rourke 1973). Nomenclature of plant species follows Flora of the Great Plains (1986).

Results

Effects of Previous Management

The mixed grass prairie ecosystems on the study area degraded because the previous management was designed for the intended "use" and did not meet the biological requirements of the perennial native grass plants and the rhizosphere organisms and was detrimental to the biogeochemical processes. The use of rangeland natural resources should not be the objective of management. The management should be the means to accomplish the uses.

Ecosystem processes functioned at some degree less than potential level each growing season that the rangeland was managed with traditional concepts based on a use. Soon after the first ecosystem process failed to function properly, the other belowground processes and mechanisms began to deteriorate. The native grass live root biomass decreased (Whitman 1974), the defoliation resistance mechanisms within grass plants diminished, the ecosystem biogeochemical processes declined, and the competitiveness of grass plant resource uptake deteriorated (Manske 2011).

The reduction of live root surface area caused a decrease in active root length for interaction with symbiotic rhizosphere organisms and caused a decrease in absorption of water and nutrients from the soil. Reduction of active root biomass and diminishment of grass plant health vigor 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 was a contributing factor in the reduction of rhizosphere biomass. The primary cause for the reduction in rhizosphere biomass was, however, the great reduction in the quantity of carbohydrates exuded from the grass roots into the rhizosphere zone. The antagonistic traditional practices greatly reduced the quantity of short carbon chain energy exuded from the grass roots into the rhizosphere; this low amount of simple carbon compounds was not enough to sustain an adequate rhizosphere biomass. The small biomass of rhizosphere organisms mineralized small quantities of nitrogen and other essential elements (Coleman et al. 1983, Klein et al. 1988).

The decreased amounts of available mineral nitrogen below 100 lbs/ac in the ecosystem caused reductions in native grass herbage biomass production (Wight and Black 1972, 1979) and caused decreases in native grass density (basal cover). As degradation continued, numerous bare spaces between native grass plants were created in the plant communities. The open spaces were ideal habitat for growth of opportunistic domesticated grass species. The composition of grass species changed with decreases in the desirable native species and increases in the less desirable domesticated species.

Standing dead leaves accumulated (Brand and Goetz 1986) as ecosystem deterioration progressed. The accumulation of live and standing dead leaves of domesticated grasses reduced light penetration greatly. Reduced sunlight to native grasses caused reduced rates of photosynthesis, decreased rates of herbage production, and increased rates of leaf senescence (Langer 1972, Briske and Richards 1995) decreasing native grass composition further. Great quantities of standing dead material did not make contact with soil preventing decomposition through microbial activity and causing litter to build up into a thick mulch layer. The thick mulch modified soil temperatures, inhibited water infiltration, and tied up carbon and nitrogen (Wright and Bailey 1982; Manske 2000, 2011). Native grasses were further inhibited by deficiencies of soil water, cool soil temperatures during spring, and reduced ecosystem nutrients caused by thick mulch.

The change in plant composition from desirable native grasses to less desirable domesticated grasses was the visible symptom of ecosystem degradation; the fundamental degradation of the ecosystem was the reduction of rhizosphere biomass, the reduction of biogeochemical processes, the reduction of available mineral nitrogen below 100 lbs/ac, and the reduction of all the other essential elements. The degree of the aboveground plant species deterioration lagged behind the degree of degradation of the belowground ecosystem processes and mechanisms (Manske 2011).

There is a major fundamental problem with traditional concepts that manage renewable natural resources from the perspective of their use or for the product removed. Management of renewable resources for a use narrowly considers only a few factors directly related to that use or product, and neglects to address the needs of all the other components required for the ecosystems to function at potential levels. The renewable natural resources (rangelands, grasslands, croplands, forestlands, and fisheries) have all been managed traditionally for their use. The ecosystem processes that renew the renewable natural resources are functioning at subpotential levels. The declining production from the worlds renewable resources is a symptom of degraded ecosystem processes that have resulted from management for a use.

Control Pasture NG

The mixed grass prairie study area in the ungrazed control pasture NG was a degraded silty ecological site dominated by kentucky bluegrass. Control pasture NG was not grazed during the six years of study. At the start of the study (May year 1), the aboveground vegetation biomass consisted of 72.3% standing dead and litter and 27.7% live herbage. The live herbage biomass was 95.2% domesticated grasses, 2.5% native grasses (2.0% cool season grasses, 0.4% upland sedges, and less than 0.1% warm season grasses), and 2.4% forbs (tables 2 and 3).

The domesticated grass herbage biomass changed little numerically throughout the study.

From a starting biomass of 1684.81 lbs/ac (95.2% composition), the weight decreased (12.8%) to 1468.69 lbs/ac (72.7% composition) during years 1 to 5, and increased (38.5%) to 2333.98 lbs/ac (85.1% composition) during year 6 (tables 2 and 3). The domesticated grass basal cover changed little during the first 4 years, greatly increased during the fifth year, and greatly decreased during the sixth year. The dominant domesticated grass was kentucky bluegrass. From a starting basal cover of 10.55% (71.3% composition), the basal cover increased (123.7%) to 23.60% (83.1% composition) during years 1 to 5, and then decreased to 15.35% (86.0% composition) during year 6 (tables 4 and 5).

The quantity of native cool season grasses was low during the study. The cool season grass herbage biomass increased slightly during the first four years and then decreased during the last two years. From a low starting biomass of 35.68 lbs/ac (2.0% composition), the weight increased (597.1%) to 248.74 lbs/ac (11.1% composition) during years 1 to 4, and then decreased (76.9%) to 57.49 lbs/ac (2.1% composition) during years 5 to 6 (tables 2 and 3). The native cool season grass basal cover increased slightly during the first three years and then decreased during the last three years. The cool season grasses were western wheatgrass, needle and thread, and green needlegrass. From a starting basal cover of 1.20% (8.1% composition), the basal cover increased (195.8%) to 3.55% (20.7% composition) during years 1 to 3, and then decreased (90.1%) to 0.35% (2.0% composition) during years 4 to 6 (tables 4 and 5).

The quantity of native warm season grasses was low during the study. The warm season grass herbage biomass changed little during the study. From an extremely low starting biomass of 0.71 lbs/ac (0.04% composition), the weight increased to 153.73 lbs/ac (5.6% composition) during years 1 to 6 (tables 2 and 3). The native warm season grass basal cover increased slightly during the study. The warm season grass remaining on the ungrazed site was a small remnant colony of prairie sandreed. From an extremely low starting basal cover of 0.05% (0.34% composition), basal cover increased a little to 0.85% (4.8% composition) during years 1 to 6 (tables 4 and 5).

The native cool and warm season grasses changed little during the study. From a low starting biomass of 36.39 lbs/ac (2.1% composition), the weight increased to 304.91 lbs/ac (13.6% composition) during years 1 to 4 and then decreased to 211.22 lbs/ac (7.7% composition) during years 5 to 6 (tables 2 and 3). The total cool and warm season grass basal cover increased slightly during the first three years, and then decreased slightly during the last three years. From a low starting basal cover of 1.25% (0.34% composition), the basal cover increased (216.09%) to 3.95% (23.0% composition) during years 1 to 3, and the decreased (69.6%) to 1.20% (6.7% composition) during years 4 to 6 (tables 4 and 5).

The quantity of upland sedges was low during the study. The upland sedge herbage biomass increased slightly during the first four years and then decreased during the last two years. From a low starting biomass of 7.14 lbs/ac (0.4% composition), the weight increased to 49.44 lbs/ac (2.2% composition) during years 1 to 4, and then decreased to 11.82 lbs/ac (0.4% composition) during years 5 to 6 (tables 2 and 3). The upland sedge basal cover decreased during the study. The upland sedge was primarily threadleaf sedge. From a starting basal cover of 2.85% (19.3% composition), the basal cover decreased (63.2%) to 1.05% (5.9% composition) during years 1 to 6 (tables 4 and 5).

The quantity of forbs was low during the study. The forb herbage biomass decreased during the first three years, increased during the fourth and fifth years, and then decreased during the sixth year. From a low starting biomass of 42.10 lbs/ac (2.4% composition), the weight decreased (35.8%) to 27.02 lbs/ac (1.8% composition) during years 1 to 3, the weight increased (783.2%) to 238.65 lbs/ac (11.8% composition) during years 4 to 5, and the weight decreased (22.3%) to 185.43 lbs/ac (6.8% composition) during year 6 (tables 2 and 3). Forb density decreased during the first three years and increased during the last three years. From a starting density of 5.44 forbs/0.10 m^2, the density decreased (89.7%) to 0.56 forbs/0.10 m^2 during years 1 to 3, and the density increased (535.7%) to 3.56 forbs/0.10 m^2 during years 4 to 6.

Standing dead biomass was 1824.68 lbs/ac (28.6% composition) at the start of the study, decreasing (76.3%) to 432.54 lbs/ac (11.0% composition) during years 1 to 5, and then increasing (184.1%) to 1229.02 lbs/ac (17.2% composition) during year 6. Litter biomass was 2785.89 lbs/ac (43.7% composition) at the start of the study, decreased (47.0%) to 1476.03 lbs/ac (37.6% composition) during years 1 to 5, and then increased (115.4%) to 3178.78 lbs/ac (44.5% composition) during year 6. The litter layer was very thick during each year on the ungrazed control pasture. The biomass of the litter was greater during the sixth year than during the first year. The mean annual litter biomass was 2356.04 lbs/ac (43.4% composition). Total dead biomass (standing dead and litter) was 4610.57 lbs/ac (72.3% composition) at the start of the study, the biomass decreased (58.6%) to 1908.57 lbs/ac (48.6% composition) during years 1 to 5, and then increased (130.9%) to 4407.80 lbs/ac (61.7% composition) during year 6. The mean annual total dead biomass was 3356.59 lbs/ac (61.8% composition).

After 6 growing seasons on the ungrazed control pasture NG, the aboveground vegetation biomass consisted of 61.7% standing dead and litter and 38.3% live herbage. The live herbage was 85.1% domesticated grasses, 8.1% native grasses (5.6% warm season grasses, 2.1% cool season grasses, and 0.4% upland sedges), and 6.8% forbs (table 3).

The vegetation on control pasture NG changed slightly during the 6 years of nongrazing management. Domesticated grass herbage biomass increased 38.5% and basal cover increased 45.5%. Cool season grass herbage biomass increased 61.1% and basal cover decreased 70.8%. Warm season grass herbage biomass increased 2155.1% and basal cover increased 1600.0%. Upland sedge herbage biomass increased 65.5% and basal cover decreased 63.2%. Forb herbage biomass increased 340.5% and density decreased 34.6%. Total live herbage biomass increased 54.9% and total live basal cover increased 20.6%. Standing dead herbage biomass decreased 32.6% and litter biomass increased 14.1%.

The total available soil mineral nitrogen was 81.36 lbs/ac. The quantity of nitrate was 10.50 lbs/ac and the quantity of ammonium was 70.86 lbs/ac. The amount of available mineral nitrogen was high, indicating that the level of plant growth was reduced and the rate of available mineral nitrogen use was also reduced. The high quantities of nitrate appear to be related to the greater quantities of easily decomposed labile roots of domesticated grasses. The ungrazed control pasture had high domesticated grass basal cover. The high quantities of ammonium are usually related to greater quantities of native grass roots and greater rhizosphere biomass. However, the ungrazed control pasture had extremely low basal cover of native grasses. The ungrazed control pasture did have high kentucky bluegrass basal cover. It appears that the high quantity of ammonium on the ungrazed control pasture could be related to the easily decomposed labile roots of kentucky bluegrass with low rhizosphere biomass.

The domesticated grasses and native grasses on the ungrazed control pasture responded to water stress at different levels. The amount of precipitation during the first three years was a little less than 75% of the long-term mean resulting in early stages of water stress. The domesticated grasses were under water stress and the herbage biomass production decreased (21.6%) to 1320.16 lbs/ac. The native grasses, however, were not under as much water stress and the reduction of domesticated grass herbage biomass permitted the native grasses to increase production (273.9%) to 162.75 lbs/ac during the first three years with low precipitation.

The amount of precipitation during the last three years was greater at about 95% of the long-term mean. The domesticated grasses were no longer under water stress and the herbage biomass production increased (76.8%) to 2333.98 lbs/ac. The increased domesticated grass herbage biomass increased the shading effect on most of the smaller native grasses and caused a reduction in herbage biomass. However, a small remnant colony of prairie sandreed, a tall native grass, was able to grow above the shading by the domesticated grass leaves and was able to produce some herbage biomass at 223.05 lbs/ac which was an increase of 37.1% greater than the native grass herbage biomass production during the three years with low precipitation.

Nondefoliated live and standing dead leaves of grasses accumulated on the ungrazed control pasture NG and greatly reduced light penetration. Grass plants produce double the quantity of leaf biomass than needed for normal plant growth and maintenance as an evolutionary survival mechanism in response to partial defoliation and the loss of leaf area as forage to grazing graminivores (Crider 1955, Coyne et al. 1995). This mechanism does not stop on ungrazed pastures. Without grazing graminivores to remove half of the annual herbage production, the surplus leaf material accumulated rapidly and changed from an asset to a detriment. The accumulation of overstory vegetation reduced light penetration below native grass light saturation points (Peltzer and Kochy 2001). Native grasses have high light saturation points and require near full sunlight. Warm season grasses have higher light saturation points than cool season grasses (Kochy 1999, Kochy and Wilson 2000). Shading reduces native warm season grasses more than native cool season grasses. Introduced cool season domesticated grasses have lower light saturation points than native grasses, permitting domesticated grasses to live in low light conditions.

Low amounts of sunlight reaching native grass leaves decreased the rate of photosynthesis, which reduced the quantity of atmospheric carbon dioxide fixed, reducing the quantity of simple carbohydrates produced (Coyne et al. 1995). Low quantities of carbohydrates cause decreases in growth of roots, leaves, and stems, and in the development of secondary tillers. Low quantities of carbohydrates also cause increases in the rates of leaf senescence and increases in tiller mortality that result in reductions of native grass plant density (basal cover) and reductions of herbage biomass production (Langer 1972, Grant et al. 1983, Briske and Richards 1995).

The standing dead biomass on ungrazed pastures rapidly accumulated and the resulting tanglement of leaves and stems could not make contact with the soil surface and decompose quickly through microbial activity. The standing dead biomass decreased slowly by leaching and weathering and built up into a thick mulch layer. Thick mulch effectively blocked sunlight from reaching understory young grass leaves. Thick mulch insulates the soil from warm spring air temperatures preventing heating of cold soil that caused delays in plant and soil organism activity. Thick mulch ties up and holds organic nutrients above the soil surface preventing accession to the soil organic matter which limits nutrient cycling through biogeochemical processes increasing the deficiencies of essential elements. Thick mulch absorbs and holds precipitation for later evaporation preventing the water from infiltrating into the soil diminishing soil water to deficiency quantities (Wright and Bailey 1982, Manske 2000, 2011). These undesirable modifications to the ecosystem cause decreases in soil microorganism biomass and activity resulting in further reductions in the rates of organic material decomposition (Anderson et al. 1981, Curl and Truelove 1986, Whipps 1990).

The decreased supply of soil water, mineral nitrogen, and fixed carbon resulted in a major reduction in assimilation of plant tissue, reducing growth of leaves and roots, and reducing the development of vegetative secondary tillers (Langer 1972, Briske and Richards 1995). Native grass tiller mortality increased and native plant density decreased (Grant et al. 1983), creating large open spaces available for invasion by the less desirable domesticated cool season grasses, kentucky bluegrass and smooth bromegrass. The increasing live herbage biomass and increasing standing dead biomass of the invading domesticated grasses caused additional shading that resulted in accelerated reductions of the native grasses.

Grazed Pastures TOR

The mixed grass prairie study areas in grazed pastures TOR were degraded silty ecological sites dominated by kentucky bluegrass. At the start of the study (May year 1), the aboveground vegetation biomass consisted of 63.6% standing dead and litter and 36.4% live herbage. The live herbage biomass was 64.8% domesticated grasses, 26.2% native grasses (22.9% upland sedges, 2.7% cool season grasses, and 0.6% warm season grasses), and 9.0% forbs (table 7).

The domesticated grass herbage biomass decreased during the first and third years, increased slightly during the second, fourth, and fifth years, and increased greatly during the sixth year. From a pregrazing biomass of 1066.48 lbs/ac (64.8% composition), the weight decreased (35.7%) to 685.72 lbs/ac (39.8% composition) during years 1 to 5, and increased (83.9%) to 1261.24 lbs/ac (58.0% composition) during year 6 (tables 6 and 7). The domesticated grass basal cover increased during the first 5 years. The domesticated grasses were primarily kentucky bluegrass with small quantities of smooth bromegrass and crested wheatgrass. From a pregrazing basal cover of 3.45% (24.8% composition), the basal cover increased (99.4%) to 6.88% (22.7% composition) during years 1 to 5 and 6 (tables 8 and 9). Kentucky bluegrass had the greatest basal cover increase.

The native cool season grass herbage biomass increased during the first six years. From a pregrazing biomass of 43.53 lbs/ac (2.7% composition), the weight increased (1090.4%) to 518.18 lbs/ac (23.8% composition) during years 1 to 6 (tables 6 and 7). The native cool season grass basal cover increased during the first five years and then decreased during the sixth year. The primary cool season grasses were western wheatgrass, needle and thread, and prairie junegrass. From a pregrazing basal cover of 1.85% (13.3% composition), the basal cover increased (228.6%) to 6.08% (20.1% composition) during years 1 to 5, and then decreased to 3.93% (16.8% composition) during year 6 (tables 8 and 9).

The native warm season grass herbage biomass increased during the first six years. From a pregrazing biomass of 10.00 lbs/ac (0.6% composition), the weight increased (388.9%) to 48.89 lbs/ac (2.3% composition) during years 1 to 6 (tables 6 and 7). The warm season grass basal cover increased during the first six years. The primary warm season grasses were blue grama, prairie sandreed, and plains muhly. From a pregrazing basal cover of 0.43% (3.1% composition), the basal cover increased (488.4%) to 2.53% (10.8% composition) during years 1 to 6 (tables 8 and 9).

The total native cool and warm season grass herbage biomass increased during the first six years. From a pregrazing biomass of 53.53 lbs/ac (3.3% composition), the weight increased (959.3%) to 567.07 lbs/ac (26.1% composition) during years 1 to 6 (tables 6 and 7). The total native cool and warm season grass basal cover increased during the first five years, and then decreased slightly during the sixth year. From a pregrazing basal cover of 2.28% (16.4% composition), the basal cover increased (236.0%) to 7.66% (25.3% composition) during years 1 to 5, and then decreased (15.7%) to 6.46% (27.6% composition) during year 6 (tables 8 and 9).

The native upland sedge herbage biomass decreased during the first six years. From a pregrazing biomass of 377.14 lbs/ac (22.9% composition), the weight decreased (35.0%) to 245.17 lbs/ac (11.3% composition) during years 1 to 6 (tables 6 and 7). The upland sedge basal cover increased during the first five years, and then decreased during the sixth year. The upland sedge was threadleaf sedge. From a pregrazing basal cover of 7.63% (54.8% composition), the basal cover increased (66.4%) to 12.70% (41.9% composition) during years 1 to 5, and then decreased (24.8%) to 9.55% (40.9% composition) during year 6 (tables 8 and 9).

The forb species composition was dynamic on the grazed pastures. The forb herbage biomass decreased during the first three years, increased greatly during the fourth and fifth years, and then decreased during the sixth year. From a pregrazing biomass of 147.72 lbs/ac (9.0% composition), the weight decreased (76.2%) to 35.17 lbs/ac (4.3% composition) during years 1 to 3, the forb biomass increased (917.5%) to 357.87 lbs/ac (20.8% composition) during years 4 to 5, and then decreased (72.0%) to 100.11 lbs/ac (4.6% composition) during year 6 (tables 6 and 7). Forb density decreased during the first three years and then the densities of blue wild lettuce and yellow sweetclover increased greatly during the last three years. From a pregrazing density of 5.52 forbs/0.10 m^2, the density of the late, mid, and early succession forbs all decreased (76.1%) to a total density of 1.32 forbs/0.10 m^2 during years 1 to 3. The early succession forbs increased greatly by 4666.7% and 4655.6% during years 4 and 6, respectively, resulting in total forb density increases (790.9%) to 11.76 forbs/0.10 m^2 and increases (753.0%) to 11.26 forbs/0.10 m^2 during years 4 and 6, respectively.

Standing dead biomass was 1213.84 lbs/ac (26.9% composition) at the start of the study, the biomass decreased (91.2%) to 107.40 lbs/ac (4.9% composition) during years 1 to 4, and then increased (374.6%) to 509.77 lbs/ac (14.2% composition) during years 5 to 6. Litter biomass was 1661.26 lbs/ac (36.8% composition) at the start of the study, the biomass decreased (71.5%) to 473.94 lbs/ac (18.5% composition) during years 1 to 5, and then increased (89.5%) to 898.17 lbs/ac (25.1% composition) during year 6. The litter layer was not thick after the first year and the litter biomass averaged 825.60 lbs/ac during years 2 to 6. The total dead biomass (standing dead and litter) was 2875.10 lbs/ac (63.6% composition) at the start of the study, the total biomass decreased (75.0%) to 718.19 lbs/ac (32.8% composition) during years 1 to 4, and then increased (96.0%) to 1407.93 lbs/ac (39.3% composition) during years 5 to 6 (tables 6 and 7).

After 6 growing seasons managed with the twice-over rotation system, the aboveground vegetation biomass on grazed pastures TOR consisted of 39.3% standing dead and litter and 60.7% live herbage. The live herbage was 58.0% domesticated grasses, 37.4% native grasses (23.8% cool season grasses, 11.3% upland sedges, and 2.3% warm season grasses), and 4.6% forbs (table 7).

The vegetation on grazed pastures TOR changed for the better during the 6 years of twice-over rotation grazing management. Domesticated grass herbage biomass increased 18.3% and basal cover increased 99.4%. Cool season grass herbage biomass increased 109.0% and basal cover increased 112.4%. Warm season grass herbage biomass increased 388.9% and basal cover increased 488.4%. Upland sedge herbage biomass decreased 35.0% and basal cover increased 25.2%. Forb herbage biomass decreased 32.2% and forb density increased 104.0%. Total live herbage biomass increased 32.1% and total live basal cover increased 67.8%. Standing dead herbage biomass decreased 58.0% and litter biomass decreased 45.9%.

The total available soil mineral nitrogen of nitrate and ammonium was 53.78 lbs/ac on the exclosure and 56.74 lbs/ac on the grazed area, with an increase of 5.5% on the grazed area. The quantity of mineral nitrogen was greater on the grazed area than on the ungrazed exclosure. The quantity of nitrate was 6.84 lbs/ac on the exclosure and 5.67 lbs/ac on the grazed area, with a decrease of 17.1% on the grazed area. The quantity of ammonium was 46.95 lbs/ac on the exclosure and 51.08 lbs/ac on the grazed area, with an increase of 8.8% on the grazed area. The exclosure had greater nitrate and lower ammonium and the grazed area had lower nitrate and greater ammonium. The quantity of nitrate was reduced on both the exclosure and grazed area. Reduced quantities of nitrate appear to be related to reduced quantities of easily decomposed labile roots of domesticated grasses. Both the exclosure and grazed area had reduced domesticated grass basal cover. The grazed area had greater ammonium. The greater quantities of ammonium appear to be related to the greater quantities of native grass roots and greater rhizosphere biomass.

The degraded mixed grass prairie silty ecological sites on grazed pastures TOR were dominated by kentucky bluegrass with 64.8% composition. The native cool and warm season grasses had been reduced to 3.3% composition. These degraded prairie sites were managed with the twice-over rotation system for 6 years. During the first three years, heavy weight livestock with mean weight of 1450 lbs were stocked at 72.3%, 82.6%, and 107.5% of the assessed stocking rate, respectively, and the livestock consumed 394 lbs, 450 lbs, and 585 lbs of herbage weight per acre, respectively. During the first three years, standing dead biomass decreased (65.3%) to 420.37 lbs/ac, litter biomass decreased (32.9%) to 1114.80 lbs/ac, domesticated grass herbage biomass decreased (70.9%) to 310.77 lbs/ac, and total live herbage biomass decreased (49.9%) to 824.67 lbs/ac. The native cool and warm season grasses increased (295.6%) to 211.74 lbs/ac.

The near full stocking rates at a mean of 87.5% of the assessed stocking rate of the heavy weight livestock that consumed a mean of 476 lbs of herbage biomass per acre removed sufficient quantities of domesticated grass and standing dead herbage biomass to substantially reduce the shading problems, permitting sunlight to reach the shorter native grasses. Partial defoliation of the native grasses by grazing livestock during vegetative phenological stages stimulated the defoliation resistance mechanisms, activated the rhizosphere organisms, and enhanced the ecosystem biogeochemical processes resulting in increased herbage biomass production and greater vegetative tiller growth.

The stocking rate at greater than 100% of the assessed value during year 3 caused both beneficial effects and negative effects. The third growing season was the only time that grazing livestock were at great enough quantities to remove 916.93 lbs/ac of domesticated grass and standing dead biomass and open the grass leaf canopy sufficiently. Carryover effects lasted into the following grazing season during year 4. Standing dead biomass decreased (74.5%) to 107.40 lbs/ac and litter biomass decreased (45.2%) to 610.79 lbs/ac. Native cool and warm season grass herbage biomass increased (109.8%) to 444.27 lbs/ac. However, the negative factors were also great, total forb biomass increased (168.7%) to 94.50 lbs/ac and weedy forb density increased 4666.7% during the next growing season as a result of opening the grass canopy excessively and exposing sunlight on large areas of soil causing weed seeds to germinate.

During the fourth and fifth years, medium weight livestock with mean weight of 900 lbs were stocked at 79.8% and 87.4% of the assessed stocking rate, respectively, and the livestock consumed 304 lbs and 333 lbs of herbage weight per acre, respectively. The quantity of herbage biomass consumed per acre was insufficient to maintain ecosystem improvement. Standing dead biomass increased (238.6%) to 363.68 lbs/ac, domesticated grass herbage biomass increased (120.7%) to 685.72 lbs/ac, and forb herbage biomass increased (278.7%) to 357.87 lbs/ac. Native cool and warm season grass herbage biomass decreased (21.9%) to 346.76 lbs/ac.

During the sixth year, light weight livestock with mean weight of 650 lbs were stocked at 37.8% of the assessed stocking rate and the livestock consumed 113 lbs of herbage weight per acre. At this low stocking rate, the quantity of herbage biomass consumed per acre was so inadequate that ecosystem restoration stopped, causing the return of advancements of degradation. Standing dead biomass increased (40.2%) to 509.77 lbs/ac, litter biomass increased (89.5%) to 898.17 lbs/ac, domesticated grass herbage biomass increased (83.9%) to 1261.24 lbs/ac, and early succession forb density increased 256.7%. Native cool and warm season grass herbage biomass increased (63.5%) to 567.07 lbs/ac as a result of continued effects from previous beneficial partial defoliation by grazing at heavier stocking rates.

Differences in Restoration Changes

The restoration changes of the ecosystems on the ungrazed control pasture NG and on the grazed pastures TOR were different. At the start of the study, a similarity index of 52.6% indicated that the degraded plant communities on the ungrazed control pasture NG and on the grazed pastures TOR were more similar than dissimilar.

During the study, the grazing managed with twice-over rotation strategy on pastures TOR reduced the standing dead biomass 58.5% and reduced the litter biomass 71.7% below that on the ungrazed control pasture NG. This reduction in standing dead decreased the problems caused by shading that reduced the rates of photosynthesis and increased the rates of leaf senescence in native grasses. This reduction in litter decreased the problems caused by thick mulch that modified soil temperatures, inhibited water infiltration, and tied up carbon and nitrogen.

During the study, domesticated grass herbage biomass increased 649.17 lbs/ac (38.5%) and basal cover increased 4.80 percentage points (45.5%) on the ungrazed pasture NG. Domesticated grass herbage biomass increased 194.76 lbs/ac (18.3%) and basal cover increased 3.43 percentage points (99.4%) on the grazed pastures TOR. At the end of the study, domesticated grass herbage biomass was 46.0% less and basal cover was 55.2% less on the grazed pastures TOR than on the ungrazed control pasture NG. The rate of increase of domesticated grass herbage biomass and basal cover was restricted by the grazing treatment.

The combined aboveground vegetation biomass of domesticated grass and standing dead caused the shading problem and prevented most of the sunlight from reaching the smaller native grass plants growing in the understory. During the study, the annual mean combined vegetation biomass was 2617.80 lbs/ac on the ungrazed pasture NG and was significantly less at 1277.06 lbs/ac on the grazed pastures TOR. The grazing treatment reduced the shading problem 51.2% which was sufficient to permit greater amounts of sunlight to reach native grass leaves, increasing the photosynthetic rates that increased the quantities of fixed carbon available to native grasses resulting in increased growth rates. The annual mean native grass herbage biomass on the ungrazed pasture NG was only 245.28 lbs/ac and was significantly greater at 650.01 lbs/ac on the grazed pastures TOR. The grazing treatment increased the native grass production 165.0% as a result of reducing the shading problem.

At the end of the study, cool and warm season grass herbage biomass was 168.5% greater and basal cover was 438.3% greater on the grazed pastures than on the ungrazed pasture. Native upland sedge herbage biomass was 1974.2% greater and basal cover was 809.5% greater on the grazed pastures than on the ungrazed pasture. Forb herbage biomass was 46.0% less and forb density was 216.3% greater on the grazed pastures than on the ungrazed pasture.

The improvements of the native grasses in the degraded native mixed grass prairie communities on the grazed pastures TOR indicated that the defoliation resistance mechanisms were activated to some degree by the twice-over rotation grazing management strategy. Increased activity of the compensatory internal physiological growth processes resulted in increased production of native grass herbage biomass. Increased activity of the internal vegetative reproductive processes resulted in increased native grass basal cover. At the end of the study, a similarity index of 37.3% indicated that the improved plant communities on grazed pastures TOR and the degraded plant communities on ungrazed control pasture NG were more dissimilar than similar.

The previous management degraded the plant communities and caused reductions in the quantity of plant carbon exudates released into the rhizosphere that caused a decrease in rhizosphere biomass. At the start of the study, the rhizosphere biomass on ungrazed control pasture NG had decreased to 52.23 kg/m$^{3.}$ The rhizosphere biomass on grazed pastures TOR had decreased to 77.99 kg/m^3. These low quantities of rhizosphere biomass are less than 20% of the potential rhizosphere biomass of 406.44 kg/m^3 recorded on silty ecological sites managed long-term with a twice-over rotation grazing strategy.

Rhizosphere organism biomass and activity are limited by access to simple carbon chains because the microflora trophic levels lack chlorophyll and have low carbon (energy) content. Partial defoliation of grass plants at vegetative phenological growth stages by large grazing graminivores causes greater quantities of exudates containing simple carbon compounds to be released through the plant roots into the rhizosphere. With the increase in availability of carbon compounds in the rhizosphere, activity of the microorganisms increases. The increase in rhizosphere organism activity causes an increase in rhizosphere volume and biomass. Without partial defoliation by grazing at specific grass growth stages, only small quantities of plant material leak from the grass roots into the rhizosphere; this low amount of carbon compounds is barely enough to sustain a small rhizosphere biomass at less than 20% of potential biomass (Manske 1999, 2011).

During the first two years of the study, the rhizosphere weights on the grazed pastures were numerically greater than the rhizosphere weights on the ungrazed control pasture, but were not significantly different. However, the rhizosphere weights on the grazed pastures became significantly greater than those on the ungrazed pasture during years 3 to 6 (table 10 and figure 1).

The rhizosphere weights on the ungrazed control pasture NG changed little during years 1 to 5. The changes in rhizosphere weight did appear to be responses to changes in growing season precipitation. The rhizosphere weights on the ungrazed pasture were not significantly different during years 1 to 3, when the mean growing season precipitation was 10.54 inches (71.26% of LTM). The rhizosphere weights during years 4 and 5 increased slightly when the mean growing season precipitation increased slightly to 12.53 inches (84.72% of LTM). The rhizosphere weights were not significantly different from each other during years 4 and 5 but were significantly greater than the rhizosphere weights during years 1 to 3. The rhizosphere weights increased greatly when the growing season precipitation increased greatly to 17.15 inches (115.96% of LTM) during year 6. The rhizosphere weights on ungrazed pasture NG were significantly greater during year 6 than those during years 1 to 5 (table 10 and figure 1). Changes in rhizosphere weights on the ungrazed pasture appeared to be related to changes in growing season precipitation, or more specifically to changes in the availability of hydrogen, which in turn effected the quantity of atmospheric carbon fixed during photosynthesis increasing the quantity of carbohydrates. With greater quantities of plant carbohydrates, the quantity of simple carbon compounds that leaked from grass roots into the rhizosphere increased proportionally, increasing the rhizosphere biomass. During this study, the rhizosphere biomass on the ungrazed pasture changed from 12.9% to 32.1% of the potential rhizosphere biomass on long-term twice-over rotation management strategies.

The rhizosphere weights on the grazed pastures TOR did not change significantly during years 1 and 2, and the rhizosphere weights on the grazed pastures were not significantly different than those on the ungrazed pasture during the first 2 years. The rhizosphere weights increased 33% between the second and third years on the grazed pastures and continued to increase weight at a mean rate of 30.5 kg/m^3 per year from the second year to the sixth year which was 131.5% greater than the change in rhizosphere weights on the ungrazed control pasture. The rhizosphere weights on the grazed pastures were significantly greater than those on the ungrazed control pasture each year from year three to year six (table 10 and figure 1). The rhizosphere biomass increases during years three to six on the grazed pastures appeared to be related to increases in carbon exudates that resulted from partial defoliation by grazing of grass lead tillers during vegetative growth stages. During this study, the rhizosphere biomass on the grazed pastures changed from 19.2% to 52.7% of the potential rhizosphere biomass on long-term twice-over rotation management strategies.

Six years of twice-over rotation grazing management increased the rhizosphere biomass 175% and improved the plant community composition of native grasses 43%, however, neither the rhizosphere or the plant community had been fully restored and require continuation of the grazing treatment.

Discussion

Traditionally, rangeland ecosystems have been managed from the perspective of the “use” of the grassland. Livestock grazing along with watershed, wildlife, and recreation were considered to be the major uses. Management of rangelands from the perspective of a single use or for multiple uses narrowly considers only a few ecosystem components directly related with these primary uses or products removed. Management for a use does not consider rangelands as complex ecosystems and neglects to address the needs of all other ecosystem components. Management of rangelands for a use results in degradation of the ecosystems.

Rangelands are complex ecosystems consisting of numerous interactive biotic (living) and abiotic (nonliving) components. The biotic components are the plants, soil organisms, and large grazing graminivores that have biological and physiological requirements. The abiotic components require the presence of sunlight and include the essential major elements of carbon, hydrogen, nitrogen, and oxygen that have transformable characteristics between organic and inorganic forms through biogeochemical processes. Rangeland ecosystems are functioning units of coacting biotic organisms interacting with the abiotic components and the environment. The complex of mechanisms and processes connected with these extensive interactions have been collectively identified as defoliation resistance mechanisms and biogeochemical processes. If any of the numerous processes are not functioning at potential level, the ecosystem does not produce at potential levels.

Management of rangeland ecosystems needs to meet the biological and physiological requirements of the biotic components and activate the biogeochemical processes that cycle the abiotic components. Mixed grass prairie communities require biologically effective partial defoliation by annually managed grazing animals in order to persist as healthy and productive ecosystems. Thus, providing the means to accomplish the uses of watershed, wildlife habitat, recreation, and livestock forage at the same time on fully functional rangeland ecosystems.

Implementation of the biologically effective twice-over rotation grazing management strategy activates the defoliation resistance mechanisms meeting the biological and physiological requirements of the biotic components and activates the biogeochemical processes that cycle the abiotic components (Manske 2011). The three main defoliation resistance mechanisms are : compensatory internal physiological processes, internal vegetative reproduction of secondary tillers from axillary buds, and external symbiotic rhizosphere organism activity (McNaughton 1979, 1983; Coleman et al. 1983; Ingham et al. 1985; Mueller and Richards 1986; Richards et al. 1988; Briske 1991; Murphy and Briske 1992; Briske and Richards 1994, 1995; Manske 2009, 2011).

The defoliation resistance mechanisms developed early during the coevolution of grass plants and grazing graminivores (McNaughton 1979, 1983; Coleman et al. 1983; Briske 1991; Briske and Richards 1995; Manske 1999, 2011) and are a complex assemblage of biogeochemical and physiological processes that involve intricate interactions among rhizosphere microorganisms, grass plants, and large grazing graminivores. Activation of these mechanisms provides important biological and physiological processes permitting native grasses to produce greater herbage biomass and to increase basal cover; these mechanisms also enable grass plants to replace lost leaf material, to restore disrupted physiological processes, and to vegetatively reproduce secondary tillers from axillary buds after partial defoliation by grazing. The defoliation resistance mechanisms function at variable levels of activation depending on the quantity of available mineral nitrogen in the ecosystem soil and on the quantity of available recently fixed carbon (Richards and Caldwell 1985). When mineral nitrogen is available at 100 lbs/ac or greater, the defoliation resistance mechanisms function at full activation. When mineral nitrogen is available at less than 100 lbs/ac, the defoliation resistance mechanisms function at levels less than full activation (Manske 2009). In addition, the water (precipitation) use efficiency processes decrease in grass plants growing in ecosystems with less than 100 lbs/ac available mineral nitrogen causing herbage biomass production to be reduced by 49.6% (Wight and Black 1972, 1979).

The quantity of available mineral nitrogen in grassland ecosystem soils is dependant on the rate of mineralization of soil organic nitrogen by rhizosphere organisms. The larger the rhizosphere volume and microorganism biomass, the greater the quantity of soil mineral nitrogen converted. Rhizosphere volume and microorganism biomass are limited by access to simple carbohydrates (Curl and Truelove 1986). Healthy grass plants capture and fix carbon during photosynthesis and produce carbohydrates in quantities greater than the amount needed for tiller growth and development (Coyne et al. 1995). Partial defoliation of grass lead tillers at vegetative physiological growth stages by large grazing graminivores causes greater quantities of exudates containing simple carbohydrates to be released from the grass tillers through the roots into the rhizosphere (Hamilton and Frank 2001). With the increase in availability of carbon compounds in the rhizosphere, the biomass and activity of the microorganisms increases (Anderson et al. 1981, Curl and Truelove 1986, Whipps 1990). The increase in rhizosphere organism biomass and activity results in greater rates of mineralization of soil organic nitrogen converting greater quantities of available mineral nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005). Mineral nitrogen available in quantities of 100 lbs/ac or greater allows partially defoliated grass tillers full activation of the defoliation resistance mechanisms (Manske 2009). Full activation of the compensatory internal physiological processes within grass plants accelerates growth rates of replacement roots, leaves, and shoots, increases photosynthetic capacity of remaining mature leaves, increases allocation of carbon and nitrogen, improves water (precipitation) use efficiency, and increases restoration of biological and physiological processes enabling rapid and complete recovery of partially defoliated grass tillers. Full activation of the asexual internal processes of vegetative reproduction increases secondary tiller development from axillary buds and increases initiated tiller density during the grazing season. Full activation of the external symbiotic rhizosphere organism activity increases mineralization of inorganic nitrogen, increases ecosystem biogeochemical cycling of essential elements, and improves belowground resource uptake competitiveness (Wight and Black 1972, 1979; McNaughton 1979, 1983; Coleman et al. 1983; Ingham et al. 1985; Mueller and Richards 1986; Richards et al. 1988; Briske 1991; Murphy and Briske 1992; Briske and Richards 1994, 1995; Manske 1999, 2011; Kochy and Wilson 2000).

Restoration of degraded mixed grass prairie ecosystems depends on the successfulness of recovery of the biogeochemical processes and revival of the indispensable component resources. The rhizosphere organism biomass must be improved initially to increase mineralization of nitrogen and other essential elements. Rhizosphere organisms increase when greater quantities of short carbon chain energy are exudated by partial defoliation by grazing. Two growing seasons are required before substantial increases in rhizosphere biomass occur. The rhizosphere biomass continues to increase as the quantity of short carbon chain energy exudated from native grasses increases.

Removal of substantial quantities of the overstory vegetation comprised of domesticated grass live and standing dead herbage biomass increases sunlight intensities reaching the understory native grass leaves sufficiently to enhance the photosynthetic rates and to increase the quantity of available fixed carbon. Reduction of adequate quantities of overstory vegetation requires grazing graminivores at relatively high stocking rates, around 85% to 100% of the assessed level. Stocking rates greater than 100% of assessed level can remove great quantities of overstory vegetation in a short time period. However, because native grass plants cannot fill the plant community open spaces rapidly, exposure of sunlight to large proportions of bare ground causes negative effects that initiate extreme increases in weedy forbs that remain problems for several years. Stocking rates less than 85% of assessed level remove insufficient quantities of overstory vegetation to effectively reduce the shading problem. Native grasses in the understory receiving insufficient sunlight continue to decline. Stocking rates between 85% and 100% of the assessed level remove enough overstory vegetation to permit an increased intensity of sunlight to reach the leaves of native grasses that increases the photosynthetic rates and fixes carbon at greater quantities sufficient for increased grass growth to progress at reasonable restoration rates.

Dead plant material does not decompose through microbial activity unless it makes contact with soil. Livestock do not preferentially consume old dead litter. However, the presence of the livestock caused greater proportions of the thick mulch to make soil contact and reduce the litter mulch biomass by greater than 70% of the litter biomass on areas without livestock.

Restoration of mixed grass prairie ecosystems degraded by traditional management concepts requires implementation of a biologically effective grazing management strategy that activates the ecosystem biogeochemical processes and the defoliation resistance mechanisms. The activation trigger for these processes and mechanisms is partial defoliation by large grazing graminivores that removes 25% to 33% of the aboveground leaf biomass from grass lead tillers at vegetative growth stages between the 3.5 new leaf stage and the flower (anthesis) stage (Manske 1999, 2011). In addition, reduction of the shading problem and of the thick mulch problem will assist the restoration process. Following recovery of some of the biogeochemical processes, the previously deficient quantities of available mineral nitrogen, essential elements, fixed carbon, and soil water start increasing upwards towards functional quantities. With the increase of component resources, native grass plants are able to synthesize increasing quantities of carbohydrates, proteins, and nucleic acids. Activation of the defoliation resistance mechanisms provides important biological and physiological processes permitting native grasses to use the vital organic compounds in increasing quantities for the production of herbage biomass and basal cover. Within a few years, the composition of native grasses increases in the plant community and becomes the dominant vegetation. The native grasses improve in competitiveness for the belowground resources of soil water, mineral nitrogen, and other essential elements which eventually reduces the remaining introduced domesticated grasses to minor composition in the plant community. The length of time required to reach recovery is related exponentially to the severity of degradation. The belowground ecosystem processes and mechanisms must be restored before the aboveground plant community can be restored.

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Table 1. Precipitation in inches for growing season months for 2006-2011, Richardton, North Dakota.

	Apr	May	Jun	Jul	Aug	Sep	Oct	Growing Season
Long-term mean (1971-2000)	1.75	2.49	3.39	2.27	1.88	1.60	1.41	14.79
2006	2.53	0.60	0.37	0.79	1.40	2.33	1.40	9.42
% of LTM	144.57	24.10	10.91	34.80	74.47	145.63	99.29	63.69
2007	1.04	3.57	2.22	0.44	1.57	1.29	0.62	10.75
% of LTM	59.43	143.37	65.49	19.38	83.51	80.63	43.97	72.68
2008	0.45	1.32	3.93	2.04	0.56	1.70	1.45	11.45
% of LTM	25.71	53.01	115.93	89.87	29.79	106.25	102.84	77.42
2009	0.59	0.85	3.09	2.82	0.53	1.67	2.08	11.63
% of LTM	33.71	34.14	91.15	124.23	28.19	104.38	147.52	78.63
2010	0.71	3.29	4.35	1.42	0.90	2.30	0.46	13.43
% of LTM	40.57	132.13	128.32	62.56	47.87	143.75	32.62	90.80
2011	2.01	4.94	1.76	4.06	2.07	0.96	1.35	17.15
% of LTM	114.86	198.39	51.92	178.85	110.11	60.00	95.74	115.96
2006-2011	1.22	2.43	2.62	1.93	1.17	1.71	1.23	12.31
% of LTM	69.71	97.59	77.28	85.02	62.23	106.88	87.23	83.23

Table 2. Mean herbage biomass (lbs/ac) for nongrazed silty native rangeland sites dominated by kentucky bluegrass.

Pasture NG	Pregrazing	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
Domesticated	1684.81	1833.85	1791.31	1320.16	1779.62	1468.69	2333.98
Cool Season	35.68	73.30	110.22	97.30	248.74	180.95	57.49
Warm Season	0.71	59.02	126.59	45.16	56.17	102.76	153.73
Native Grass	36.39	132.32	236.81	142.46	304.91	283.71	211.22
Sedges	7.14	25.91	22.27	20.29	49.44	30.48	11.82
Forbs	42.10	128.75	75.97	27.02	116.81	238.65	185.43
Total Live	1770.44	2120.83	2126.36	1509.93	2250.78	2021.53	2742.47
Standing Dead	1824.68	1381.12	708.48	928.70	499.32	432.54	1229.02
Litter	2785.89	2452.03	2131.29	2521.86	1946.39	1476.03	3178.78
Total Dead	4610.57	3833.15	2839.77	3450.56	2445.71	1908.57	4407.80
Total Biomass	6381.01	5953.98	4966.13	4960.49	4696.49	3930.10	7150.27

Table 3. Percent composition of herbage biomass for nongrazed silty native rangeland sites dominated by kentucky bluegrass.

Pasture NG	Pregrazing	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
Domesticated	95.16	86.47	84.24	87.43	79.07	72.65	85.11
Cool Season	2.02	3.46	5.18	6.44	11.05	8.95	2.10
Warm Season	0.04	2.78	5.95	2.99	2.50	5.08	5.61
Native Grass	2.06	6.24	11.13	9.43	13.55	14.03	7.71
Sedges	0.40	1.22	1.05	1.34	2.20	1.51	0.43
Forbs	2.38	6.07	3.57	1.79	5.19	11.81	6.76
Total Live	27.75	35.62	42.82	30.44	47.92	51.44	38.35
Standing Dead	28.60	23.20	14.27	18.72	10.63	11.01	17.19
Litter	43.66	41.18	42.92	50.84	41.44	37.56	44.46
Total Dead	72.25	64.38	57.18	69.56	52.08	48.56	61.65

Table 4. Basal cover (%) for nongrazed silty native rangeland sites dominated by kentucky bluegrass.

Pasture NG	Pregrazing	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
Domesticated	10.55	12.35	19.95	11.20	15.30	23.60	15.35
Cool Season	1.20	0.40	2.30	3.55	0.70	1.25	0.35
Warm Season	0.05	0.50	0.80	0.40	0.55	0.65	0.85
Native Grass	1.25	0.90	3.10	3.95	1.25	1.90	1.20
Sedges	2.85	2.00	2.20	1.90	2.35	1.75	1.05
Forbs	0.05	0.80	0.30	0.10	0.10	1.15	0.20
Total Live	14.80	16.05	25.55	17.15	19.00	28.40	17.85
Litter	85.20	83.95	74.45	82.85	81.00	71.60	82.15
Total	100.00	100.00	100.00	100.00	100.00	100.00	100.00

Table 5. Percentage composition (%) of basal cover for nongrazed silty native rangeland sites dominated by kentucky bluegrass.

Pasture NG	Pregrazing	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
Domesticated	71.28	76.95	78.08	65.31	80.53	83.10	85.99
Cool Season	8.11	2.49	9.00	20.70	3.68	4.40	1.96
Warm Season	0.34	3.12	3.13	2.33	2.89	2.29	4.76
Native Grass	8.45	5.61	12.13	23.03	6.57	6.69	6.72
Sedges	19.26	12.46	8.61	11.08	12.37	6.16	5.88
Forbs	0.34	4.98	1.17	0.58	0.53	4.05	1.12
Total Live	14.80	16.05	25.55	17.15	19.00	28.40	17.85
Litter	85.20	83.95	74.45	82.85	81.00	71.60	82.15

Table 6. Mean herbage biomass (lbs/ac) for grazed silty native rangeland sites dominated by kentucky bluegrass.

Pastures TOR	Pregrazing	Year1	Year 2	Year 3	Year 4	Year 5	Year 6
Domesticated	1066.48	954.70	1156.08	310.77	547.59	685.72	1261.24
Cool Season	43.53	177.90	300.19	188.95	395.69	307.77	518.18
Warm Season	10.00	28.19	42.21	22.79	48.58	38.99	48.89
Native Grass	53.53	206.09	342.40	211.74	444.27	346.76	567.07
Sedges	377.14	287.58	264.50	266.99	382.80	334.68	245.17
Forbs	147.72	122.28	77.06	35.17	94.50	357.87	100.11
Total Live	1644.85	1570.64	1840.03	824.67	1469.15	1725.02	2173.57
Standing Dead	1231.84	853.06	491.99	420.37	107.40	363.68	509.77
Litter	1661.26	1479.24	1030.31	1114.80	610.79	473.94	898.17
Total Dead	2875.10	2332.30	1522.30	1535.16	718.19	837.62	1407.93
Total Biomass	4520.05	3902.94	3362.33	2359.83	2187.34	2562.64	3581.51

Table 7. Percent composition of herbage biomass for grazed silty native rangeland sites dominated by kentucky bluegrass.

Pastures TOR	Pregrazing	Year1	Year 2	Year 3	Year 4	Year 5	Year 6
Domesticated	64.84	60.78	62.83	37.68	37.27	39.75	58.03
Cool Season	2.65	11.33	16.31	22.91	26.93	17.84	23.84
Warm Season	0.61	1.79	2.29	2.76	3.31	2.26	2.25
Native Grass	3.25	13.12	18.61	25.68	30.24	20.10	26.09
Sedges	22.93	18.31	14.37	32.38	26.06	19.40	11.28
Forbs	8.98	7.79	4.19	4.26	6.43	20.75	4.61
Total Live	36.39	40.24	54.72	34.95	67.17	67.31	60.69
Standing Dead	26.85	21.86	14.63	17.81	4.91	14.19	14.23
Litter	36.76	37.90	30.64	47.24	27.92	18.49	25.08
Total Dead	63.61	59.76	45.28	65.05	32.83	32.69	39.31

Table 8. Basal cover (%) for grazed silty native rangeland sites dominated by kentucky bluegrass.

Pastures TOR	Pregrazing	Year1	Year 2	Year 3	Year 4	Year 5	Year 6
Domesticated	3.45	4.80	5.35	4.08	6.20	6.88	6.88
Cool Season	1.85	1.85	6.83	4.08	4.98	6.08	3.93
Warm Season	0.43	0.70	1.83	2.73	2.63	1.58	2.53
Native Grass	2.28	2.55	8.66	6.81	7.61	7.66	6.46
Sedges	7.63	7.75	10.83	10.75	11.05	12.70	9.55
Forbs	0.58	0.45	0.43	0.20	0.45	3.05	0.50
Total Live	13.93	15.55	25.25	21.83	25.30	30.28	23.38
Litter	85.90	84.43	74.75	78.18	74.70	69.73	76.63
Total	99.83	99.98	100.00	100.00	100.00	100.00	100.00

Table 9. Percentage composition (%) of basal cover for grazed silty native rangeland sites dominated by kentucky bluegrass.

Pastures TOR	Pregrazing	Year1	Year 2	Year 3	Year 4	Year 5	Year 6
Domesticated	24.77	30.87	21.19	18.69	24.51	22.72	29.43
Cool Season	13.28	11.90	27.05	18.69	19.68	20.08	16.81
Warm Season	3.09	4.50	7.25	12.51	10.40	5.22	10.82
Native Grass	16.37	16.40	34.30	31.20	30.08	25.30	27.63
Sedges	54.77	49.84	42.89	49.24	43.68	41.94	40.85
Forbs	4.16	2.89	1.70	0.92	1.78	10.07	2.14
Total Live	13.93	15.55	25.25	21.83	25.30	30.28	23.38
Litter	85.90	84.43	74.75	78.18	74.70	69.73	76.63

Table 10. Rhizosphere weight (kg/m^3) for the control pasture and grazed pastures during six years of twice-over rotation management.

	Control Pasture kg/m^3	Grazed Pastures kg/m^3	% Difference
Pregrazing	52.23	77.99	49.32
Year 1	64.24x	83.28x	29.64
Year 2	77.82x	92.22x	18.50
Year 3	70.67y	122.61x	73.50
Year 4	82.88y	140.32x	69.31
Year 5	86.85y	183.00x	110.71
Year 6	130.56y	214.34x	64.17

Means in the same row and followed by the same letter (x, y) are not significantly different ($P<0.05$).

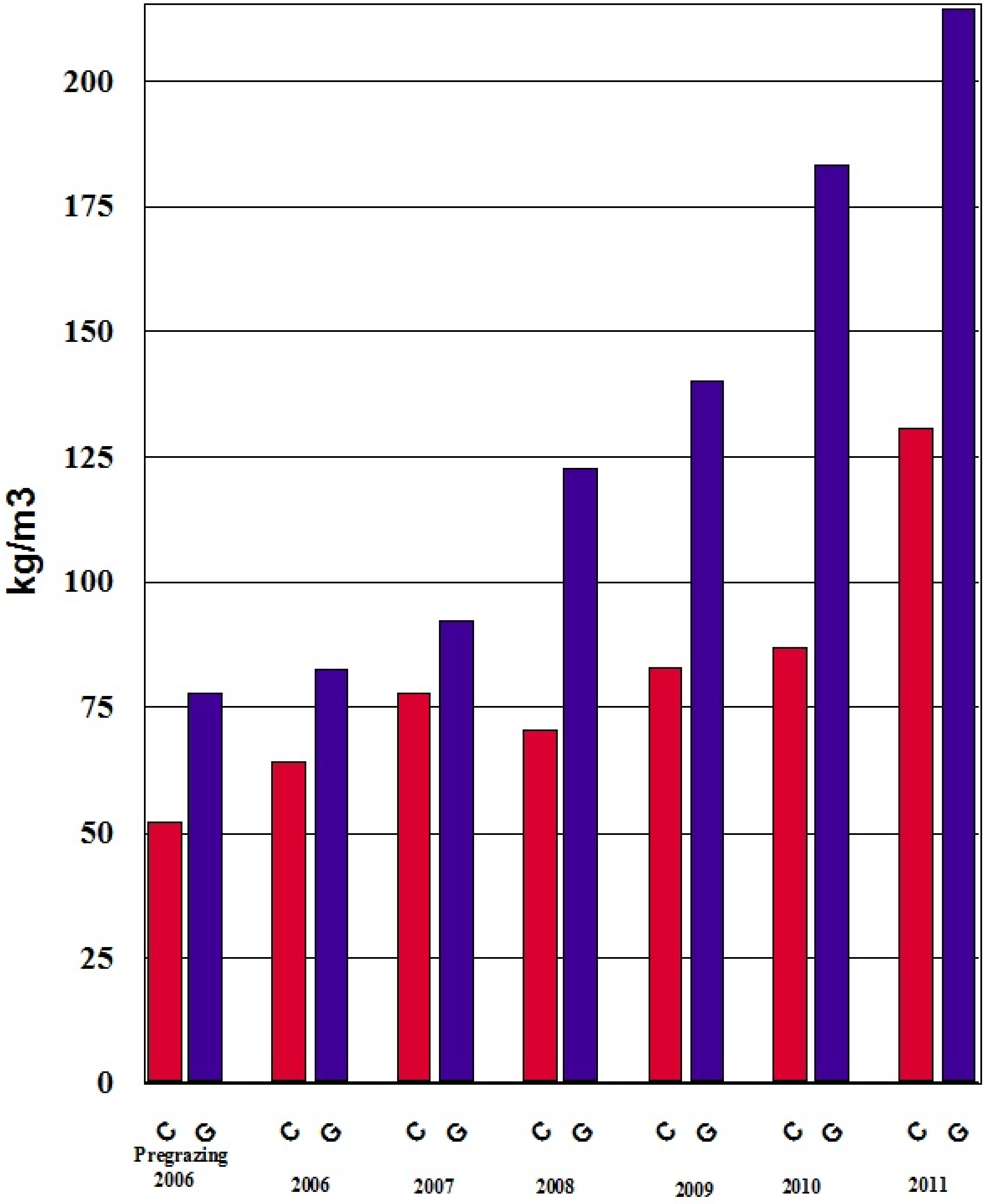

Figure 1. Rhizosphere weight (kg/m3) for the control pasture (red) and grazed pastures (blue) during six years of twice-over rotation management, 2006-2011.

Literature Cited

Anderson, R.V., D.C. Coleman, C.V. Cole, and E.T. Elliott. 1981. Effect of nematodes Acrobeloides sp. and Mesodiplogaster lheritieri on substrate utilization and nitrogen and phosphorus mineralization. Ecology 62:549-555.

Bird, S.B., J.E. Herrick, M.M. Wander, and S.F. Wright. 2002. Spatial heterogeneity of aggregate stability and soil carbon in semi-arid rangeland. Environmental Pollution 116:445-455.

Brand, M.D., and H. Goetz. 1986. Vegetation of exclosures in southwestern North Dakota. Journal of Range Management 39:434-437.

Briske, D.D. 1991. Developmental morphology and physiology of grasses. p. 85-108. in R.K. Heitschmidt and J.W. Stuth (eds.). Grazing management: an ecological perspective. Timber Press, Portland, OR.

Briske, D.D., and J.H. Richards. 1994. Physiological responses of individual plants to grazing: current status and ecological significance. p. 147-176. in M. Vavra, W.A. Laycock, and R.D. Pieper (eds.). Ecological implications of livestock herbivory in the west. Society for Range Management, Denver, CO.

Briske, D.D., and J.H. Richards. 1995. Plant response to defoliation: a physiological, morphological, and demographic evaluation. p. 635-710. in D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Burrows, R.L., and F.L. Pfleger. 2002. Arbuscular mycorrhizal fungi respond to increasing plant diversity. Canadian Journal of Botany 80:120-130.

Coleman, D.C., C.P.P. Reid, and C.V. Cole. 1983. Biological strategies of nutrient cycling in soil ecosystems. Advances in Ecological Research 13:1-55.

Cook, C.W., and J. Stubbendieck. 1986. Range research: basic problems and techniques. Society for Range Management, Denver, CO. 317p.

Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995. Carbon and nitrogen dynamics in range plants. p. 59-167. in D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Crider, F.J. 1955. Root-growth stoppage resulting from defoliation of grass. USDA Technical Bulletin 1102.

Curl, E.A., and B. Truelove. 1986. The rhizosphere. Springer-Verlag, New York, NY.

Driver, J.D., W.E. Holben, and M.C. Rillig. 2005. Characterization of glomalin as a hyphal wall component of arbuscular mycorrhizal fungi. Soil Biology and Biochemistry 37:101-106.

Emberger, C., H. Gaussen, M. Kassas, and A. dePhilippis. 1963. Bioclimatic map of the Mediterranean Zone, explanatory notes. UNESCO-FAO. Paris. 58p.

Grant, S.A., G.T. Barthram, L. Torvell, J. King, and H.K. Smith. 1983. Sward management, lamina turnover and tiller population density in continuously stocked *Lolium perenne*-dominated swards. Grass and Forage Science 38:333-344.

Great Plains Flora Association. 1986. Flora of the Great Plains. University of Kansas, Lawrence, KS.

Hamilton, III, E.W., and D.A. Frank. 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82:2397-2402.

Ingham, R.E., J.A. Trofymow, E.R. Ingham, and D.C. Coleman. 1985. Interactions of bacteria, fungi, and the nemotode grazers: effects of nutrient cycling and plant growth. Ecological Monographs 55:119-140.

Klein, D.A., B.A. Frederick, M. Biondini, and M.J. Trlica. 1988. Rhizosphere microorganism effects on soluble amino acids, sugars, and organic acids in the root zone of Agropyron cristatum, A. smithii, and Bouteloua gracilis. Plant and Soil 110:19-25.

Kochy, M., and S.D. Wilson. 2000. Competitive effects of shrubs and grasses in prairie. Oikos 91:385-395.

Kochy, M. 1999. Grass-tree interactions in western Canada. Ph.D. Dissertation. University of Regina. Regina, Saskatchewan, Canada.

Langer, R.H.M. 1972. How grasses grow. Edward Arnold, London, Great Britain.

Li, X., and S.D. Wilson. 1998. Facilitation among woody plants establishing in an old field. Ecology 79:2694-2705.

Manske, L.L. 1999. Can native prairie be sustained under livestock grazing? Provincial Museum of Alberta. Natural History Occasional Paper No. 24. Edmonton, Alberta. p. 99-108.

Manske, L.L. 2000. Management of Northern Great Plains prairie based on biological requirements of the plants. NDSU Dickinson Research Extension Center. Range Science Report DREC 00-1028. Dickinson, ND. 12p.

Manske, L.L. 2003. Effects of fall grazing on grass-leaf height. NDSU Dickinson Research Extension Center. Range Management Report DREC 03-1031b. Dickinson, ND. 7p.

Manske, L.L. 2007. Effects on vegetation, endomycorrhizal fungi, and soil mineral nitrogen from prescribed burning treatments repeated every-other-year in mixed grass prairie invaded by western snowberry. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 07-3044. Dickinson, ND. 19p.

Manske, L.L. 2009. Grass plant responses to defoliation. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1074. Dickinson, ND. 47p.

Manske, L.L., S. Schneider, J.A. Urban, and J.J. Kubik. 2010. Plant water stress frequency and periodicity in western North Dakota. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1077. Dickinson, ND. 11p.

Manske, L.L. 2011. Biology of defoliation by grazing. NDSU Dickinson Research Extension Center. Range Management Report DREC 11-1067b. Dickinson, ND. 25p.

Manske, L.L., and J.A. Urban. 2012. Humane soil beastie catcher: Its fabrication and use. NDSU Dickinson Research Extension Center. Range Research Report DREC 12-1079. Dickinson, ND. 9p.

McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist 113:691-703.

McNaughton, S.J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329-336.

Mosteller, F., and R.E.K. Rourke. 1973. Sturdy Statistics. Addison-Wesley Publishing Co., MA. 395p.

Mueller, R.J., and J.H. Richards. 1986. Morphological analysis of tillering in Agropyron spicatum and Agropyron desertorum. Annuals of Botany 58:911-921.

Murphy, J.S., and D.D. Briske. 1992. Regulation of tillering by apical dominance: chronology, interpretive value, and current perspectives. Journal of Range Management 45:419-429.

Peltzer, D.A., and M. Kochy. 2001. Competitive effects of grasses and woody plants in mixed grass prairie. Journal of Ecology 89:519-527.

Richards, J.H., and M.M. Caldwell. 1985. Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: a field study with *Agropyron* species. Journal of Applied Ecology 22:907-920.

Richards, J.H., R.J. Mueller, and J.J. Mott. 1988. Tillering in tussock grasses in relation to defoliation and apical bud removal. Annals of Botany 62:173-179.

Rillig, M.C., S.F. Wright, and V.T. Eviner. 2002. The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. Plant and Soil 238:325-333.

Whipps, J.M. 1990. Carbon economy. p. 59-97. in J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

Whitman, W.C. 1974. Influence of grazing on the microclimate of mixed grass prairie. p. 207-218. *in* Plant Morphogenesis as the basis for scientific management of range resources. USDA Miscellaneous Publication 1271.

Wight, J.R., and A.L. Black. 1972. Energy fixation and precipitation use efficiency in a fertilized rangeland ecosystem of the Northern Great Plains. Journal of Range Management 25:376-380.

Wight, J.R., and A.L. Black. 1979. Range fertilization: plant response and water use. Journal of Range Management 32:345-349.

Wright, H.A., and A.W. Bailey. 1982. Fire Ecology: United States and southern Canada. John Wiley & Sons. New York, NY.

Grazingland Management Based on Native Rangeland Ecosystem Mechanisms and Processes

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Traditional grazing management practices are based on providing forage dry matter for livestock and on the presumptive manipulation of the aboveground plant community. There are few differences among these traditional grazing practices because the belowground components are not acknowledged with credit equal to their biological importance. The actions aboveground have positive or negative effects on the belowground components. Negative changes belowground in turn cause negative changes aboveground and positive changes belowground cause positive changes aboveground. The interactions among the grass plants, rhizosphere soil microorganisms, and large grazing graminivores are complex. This report explains the mechanisms and processes of these interactions at a level conducive to the implementation of biologically effective grazing management strategies beneficial for native rangeland ecosystems.

Rangelands are complex ecosystems consisting of numerous biotic (living) and abiotic (nonliving) components. The biotic components are the grass plants, soil organisms, and grazing graminivores that have biological and physiological requirements. The abiotic components include radiant energy from sunlight and the essential major elements of carbon, hydrogen, nitrogen, and oxygen with separate but closely linked biogeochemical cycles that transform the elements between organic forms and inorganic forms, and with numerous biological, chemical, and atmospheric pathways that transfer the major essential elements into and out of the ecosystem. The minor essential elements consist of seven macrominerals and ten microminerals that are required by most living organisms. The minor elements have biogeochemical cycles or parts of cycles that transform the elements between organic and inorganic forms while they are within an ecosystem. There are numerous pathways that transfer minor essential elements out of an ecosystem. However, there are no readily available natural pathways that can transfer minor essential elements into an ecosystem. After a macromineral or a micromineral has been depleted from a rangeland ecosystem, that soil is deficient of that minor essential element. Rangeland ecosystems are functioning units of coacting biotic organisms interacting with the abiotic components and the environmental factors.

Grass plants, soil organisms, and graminivores have developed complex symbiotic relationships. The grazing graminivores depend on grass plants for nutritious forage. Grass plants depend on rhizosphere organisms for mineralization of essential elements, primarily nitrogen, from the soil organic matter. The main sources of soil organic matter are grazing animal waste and dead plant material. Rhizosphere organisms depend on grass plants for energy in the form of short carbon chains. Grass plants exudate short carbon chain energy through the roots into the rhizosphere following partial defoliation of the aboveground leaf material by grazing graminivores. Grass plants produce double the leaf biomass than is needed by the plant to provide nutritious leaf forage to the grazing graminivores.

Grass Tiller Growth

Grass plants use the 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. The shoot is the stem and leaves, and comprises repeated structural units called phytomers (Beard 1973, Dahl 1995). A phytomer consists of a leaf, with a blade and a sheath separated by a collar; a node, the location of leaf attachment to the stem; an internode, the stem between two nodes; and an axillary bud, meristematic tissue capable of developing into a new tiller (Hyder 1974, Dahl and Hyder 1977). Each tiller shoot generally produces 6 to 8 phytomers per growing season (Langer 1972, Dahl 1995). The crown of a grass tiller is the lower portion of a shoot and has two or more nodes (Dahl 1995). Fibrous roots grow from crown nodes that are located below ground. The internodes of the crown nodes associated with roots, crown tillers, and rhizome tillers do not elongate (Dahl 1995).

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). The oldest cells of a leaf are at the tip, and the youngest cells are at the base (Langer 1972, Dahl 1995). Several leaf primordia are at various stages of development at any one time. The oldest leaf is outermost, while younger leaves grow up through existing leaf sheaths (Rechenthin 1956, Beard 1973). Growth of the leaf results through cell enlargement and elongation (Esau 1960, Dahl 1995). A few new cells are produced by intercalary meristem located at the base of the blade, the base of the sheath, and the base of the internode (Esau 1960). Cell expansion occurs in the region protected by the sheaths of older leaves. When the cells emerge and are exposed to light, expansion ceases and photosynthesis and transpiration begin (Langer 1972). Once a leaf blade is fully expanded, no further growth of that blade is possible (Dahl 1995).

Individual leaves of grass tillers are relatively short lived. Young middle-aged leaves are in their prime when the rate of apparent photosynthesis is maximum and the leaves begin exporting assimilates to other parts (Langer 1972). At this point, the leaf has its greatest dry weight. Leaf senescence, or aging, begins shortly after middle age. Senescence begins at the tip, the oldest part of the leaf, and spreads downward. As senescence progresses, apparent photosynthesis and movement of assimilates from the leaf to the other parts of the plant decrease (Langer 1972). The rate of senescence occurs at about the same rate as leaf appearance but is influenced by environmental conditions. During senescence, cell constituents are mobilized and redistributed to other parts of the plant (Beard 1973). This process causes weight of the leaf to decrease (Leopold and Kriedemann 1975). The percentage of dryness in a leaf blade is an indication of the degree of senescence.

Longevity of grass tillers usually extend two growing seasons (Langer 1956, Butler and Briske 1988, Manske 2009a). Production of new leaf primordia continues until the status of the apical meristem changes from vegetative to reproductive. Sexual reproductive growth begins during the second growing season after the lead tiller has attained a certain minimum amount of vegetative development (Dahl 1995). Initiation of the reproductive growth stage is triggered by photoperiod (Roberts 1939, Leopold and Kriedemann 1975, Dahl 1995) but can be slightly modified by temperature and precipitation (McMillan 1957, Leopold and Kriedemann 1975, Dahl and Hyder 1977). Most secondary vegetative tillers initiate growth during the first growing season, overwinter, resume growth during the second subsequent growing season, become florally induced, and proceed with development of sexual reproductive structures (Briske and Richards 1995). When the florally induced grass lead tiller is between the third new leaf stage and 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). Previously formed leaf buds continue to grow and develop (Esau 1960, Langer 1972). Many domesticated cool season grasses reach the three and a half new leaf stage around late April to early or mid May. Most native cool season grasses reach the three and a half new leaf stage around early June, and most native warm season grasses reach the three and a half new leaf stage around mid June (Manske 1999a).

Grass tillers exhibit short shoot and long shoot strategies of stem elongation. Grasses with short shoots do not produce significant internode elongation during vegetative growth and the apical meristem remains below grazing or cutting height. Production of new leaf primordia continues until the apical meristem changes to reproductive status and developing leaves continue to expand until the flower stalk elongates (Dahl 1995). Grasses with long shoots elevate the apical meristem a short distance above ground level by internode elongation while still in the vegetative phase (Dahl 1995). After the apical meristem has changed from vegetative status, additional stem elongation occurs during the sexual reproductive phase. Grass species with long shoot tillers are nearly always decreased in pastures that are repeatedly grazed heavily (Branson 1953).

The flower bud primordia develop into the inflorescence, with the apical dome becoming the terminal spikelet. The first external evidence of flower stalk development is swelling of the enclosing sheath known as the “boot” stage. During the head emergence phenophase, 4 or 5 of the upper internodes, along with the attached leaf sheaths, elongate very rapidly by intercalary meristem cell development and the inflorescence reaches near maximum height. The flower (anthesis) phenophase occurs when the feathery stigmas (female parts) spread out and the anthers (male parts) are exposed (Langer 1972). Cool season grasses with the C_3 photosynthetic pathway are long day plants and reach the flower phenophase before 21 June during the period of increasing day length. Warm season grasses with the C_4 photosynthetic pathway are short day plants and reach the flower phenophase after 21 June during the period of decreasing day length and increasing night length (Weier et al. 1974, Leopold and Kriedemann 1975). The life cycle of a tiller with the apical meristem status changed to reproductive terminates during that growing season (Briske and Richards 1995).

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. 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 1999a) not sexual reproduction and the development of seedlings.

Vegetative secondary tillers develop from lead tillers by the process of tillering. A vegetative tiller is a shoot derived from growth of an axillary bud (Dahl 1995) and is a complete unit with roots, stem, and leaves. All young tillers are dependent on the lead tiller for carbohydrates until they have developed their own root systems and mature leaves (Dahl 1995). After secondary tillers become independent, they remain in vascular connection with other tillers of the grass plant (Moser 1977, Dahl and Hyder 1977, Dahl 1995). There are two types of tillering: crown tillers and rhizome or stolon tillers. Crown tillers grow vertically close to the lead tiller and within the enveloping leaf sheath, and tend to have a tufted or bunch-type growth habit (Dahl and Hyder 1977, Dahl 1995). Rhizome tillers penetrate the enveloping leaf sheath and grow horizontally below the soil surface away from the lead tiller for a distance before beginning vertical growth. Rhizome growth may be either continuous, producing tillers at progressive intervals, or terminal, producing one tiller when the apex turns up and emerges from the soil (Dahl 1995). The rhizome type of tillering results in the spreading or creeping growth habit of sod-forming plants (Dahl and Hyder 1977, Dahl 1995). If the horizontal growth is aboveground, it is a stolon (Dahl 1995). Stolons have continuous growth and form tillers at progressive nodes (Dahl 1995). Grass plants can produce both crown tillers and rhizome tillers. Generally, one tiller growth type is produced by a grass species more than the other tiller type. However, the expressivity of tiller type can be influenced by several growth factors and environmental conditions, and can be manipulated by defoliation management (Manske 2011b).

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 of lead tillers (Briske and Richards 1995). The physiological process by which the lead tiller exerts hormonal control over axillary bud growth is lead tiller (apical) dominance (Briske and Richards 1995). Tiller growth from axillary buds is inhibited indirectly by auxin, as the inhibiting hormone does not enter the axillary buds (Briske and Richards 1995). Auxin interferes with the metabolic function of cytokinin, a growth hormone (Briske and Richards 1995). Partial defoliation of young leaf material from grass tillers at phenological growth between the three and a half new leaf stage and the flower (anthesis) stage can stimulate vegetative growth of secondary tillers from axillary buds. Defoliation temporarily reduces the production of the blockage hormone, auxin (Briske and Richards 1994). This abrupt reduction of plant auxin in the lead tiller allows for cytokinin synthesis or utilization in multiple axillary buds, stimulating the development of vegetative tillers (Murphy and Briske 1992, Briske and Richards 1994). Several axillary buds develop into secondary tillers following partial defoliation of lead tillers at vegetative stages of phenological growth. Apparently, none of the developing secondary tillers have growth far enough advanced to take complete hormonal control over the other developing axillary buds (Manske 1996a).

Growth of several secondary tillers from axillary buds requires an abundant supply of carbon and nitrogen. The source of the carbon is not from stored carbohydrates, but from increased photosynthetic capacity of remaining mature leaves and rejuvenated portions of older leaves not completely senescent (Ryle and Powell 1975, Richards and Caldwell 1985, Briske and Richards 1995, Coyne et al. 1995). The quantity of leaf area required to provide adequate quantities of carbon is 67% to 75% of the predefoliation leaf area. The source of nitrogen for growth of secondary tillers from axillary buds is not from stored nitrogen but is the mineral nitrogen in the rhizosphere that the microorganisms had converted from soil organic nitrogen (Millard et al. 1990, Ourry et al. 1990). A threshold quantity of 100 pounds per acre (112 kg/ha) of mineral nitrogen needs to be available to the partially defoliated grass tillers in order for full activation of the vegetative tiller production processes (Manske 2009a, 2010b, 2011d).

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 from the potential of 5 to 8 buds. This developing secondary tiller produces auxin in the apical meristem and young developing leaves that hormonally suppresses development of additional axillary buds.

The longer axillary buds remain hormonally inhibited, the less likely they are to form tillers (Mueller and Richards 1986). The age of the meristematic tissue of the axillary buds that produce secondary tillers is the same age as the meristematic tissue that produce the lead tillers and, most likely, both the lead tiller and secondary tiller meristematic tissue was produced during the previous growing season. Axillary buds survive as long as the lead tiller remains alive. The lead tiller terminates life by senescence during the same growing season that the apical meristem changes from vegetative to reproductive status, and all unstimulated axillary buds terminate with the lead tiller.

Fall tillers are produced by cool-season grasses during the winter hardening process that starts around mid August. Warm-season grasses produce fall tiller buds that remain at or below ground level until the next growing season. The age of the meristematic tissue that produces fall tillers and fall tiller buds is one generation younger than the meristem that produced the lead tillers and secondary tillers. Secondary tillers with apical meristem remaining in the vegetative status, fall tillers, and fall tiller buds become the lead tillers and vegetative tillers during the subsequent growing season.

Longevity of grass plants in grassland ecosystems is dependent on development of tillers through vegetative production from axillary buds. Grass plant longevity of major northern species managed with traditional grazing practices is known to endure at least for 27 to 43 years (Briske and Richards 1995). Grass plant longevity would be expected to be greatly extended when biologically effective grazing management specifically designed to stimulate the vegetative tiller production mechanisms is implemented.

Rhizosphere Organisms

The rhizosphere is the narrow zone of soil around active roots of perennial grassland plants and is comprised of bacteria, protozoa, nematodes, springtails, mites, endomycorrhizal fungi (Elliot 1978, Anderson et al. 1981, Harley and Smith 1983, Curl and Truelove 1986, Whipps 1990, Campbell and Greaves 1990) and ectomycorrhizal fungi (Caesar-TonThat et al. 2001b, Manske and Caesar-TonThat 2003, Manske 2007). The activity of rhizosphere organisms increases along the trophic hierarchy, starting with the bacteria. This microflora trophic level lacks chlorophyll and has low carbon (energy) content. Bacteria are microscopic single celled saprophitic organisms that consume large quantities of soil organic matter and are one of the primary producers of the rhizosphere. Increases in biomass and activity of the bacteria elevates the concentration of carbon dioxide (CO_2) resulting in stimulation of activity in the other rhizosphere organisms. Protozoa are single-celled microorganisms that are mainly small amoeba and feed primarily on bacteria. Nematodes are a diverse group of small nonsegmented worms. Most nematodes feed primarily on bacteria or fungi, some feed on protozoa, and some eat other nematodes. Springtails are the most abundant insect in grassland soils and they travel among rhizosphere structures. Minute springtails ingest considerable quantities of soil organic matter in order to eat fungi and bacteria. Mites are small eight-legged arachnids that travel among rhizosphere structures and feed on fungi, nematodes, small insects, and other mites. Mites help distribute fungus spores and bacteria through the soil by carrying them on their exoskeleton. Endomycorrhizal fungi are the other primary producers of the rhizosphere and are achlorophyllous saprophytes that live on dead organic matter and can not fix carbon because they lack chlorophyll. The bacteria and fungi are the microflora saprotrophic organisms at the bottom of the food chain and makeup the greatest biomass of the rhizosphere. Both bacteria and fungi contain high proportions of nitrogen in relation to their carbon content. The rhizosphere organisms of the microfauna trophic levels graze on bacteria or fungi and ingest greater quantities of nitrogen than they need for a balanced diet based on energy (carbon); the excess nitrogen is excreted as ammonium (NH_4). The primary symbiotic function of the endomycorrhizal fungi is to nitrify the ammonium (NH_4) excreted by rhizosphere organisms and convert it into nitrate (NO_3), which is a form of mineral nitrogen usable by grass plants. The elevated rhizosphere organism activity caused by the increase in available carbon compounds results in a greater quantity of organic nitrogen converted into mineral nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005).

Along with the improvement of ecosystem biogeochemical processes and the resulting increase in available mineral nitrogen, the increase of mycorrhizal fungi biomass and activity benefits other grassland ecosystem functions. Endomycorrhizal fungi develop arbuscules, vesicles, and hyphae within root tissue of the host plant (Harley and Smith 1983) and secrete adhesive polysaccharides that bond soil particles around grass roots forming the structural environment for rhizosphere organisms, and the adhesive polysaccharides bind soil into aggregates resulting in increased soil pore spaces, increased water holding capacity, and increased rooting depth. Endomycorrhizal fungi also move phosphorus, other mineral nutrients, and water to the plant roots for absorption (Moorman and Reeves 1979, Harley and Smith 1983, Allen and Allen 1990, Box and Hammond 1990, Marschner 1992, Koide 1993, Marschner and Dell 1994, Smith and Read 1997).

Ectomycorrhizal fungi develop a sheath around the root with hyphae that do not enter the tissue of the host plant (Harley and Smith 1983) and secrete large amounts of adhesive polysaccharides forming water-stable aggregates in soil that are water permeable but not water soluable, and the increased soil aggregation improves soil quality, increases soil oxygenation, increases water infiltration, and decreases erodibility (Caesar-TonThat and Cochran 2000, Caesar-TonThat et al. 2001a, Caesar-TonThat et al. 2001b, Caesar-TonThat 2002, Manske and Caesar-TonThat 2003, Manske 2007).

Defoliation Resistance Mechanisms

The complex of mechanisms and processes connected with the extensive interactions of the biotic and abiotic ecosystem components collectively became the defoliation resistance mechanisms and biogeochemical processes (Manske 2011b). If any of the numerous processes do not function at potential level, the ecosystem does not produce at potential level. Management of rangeland ecosystems must meet the biological and physiological requirements of the biotic components and stimulate the biogeochemical processes that cycle the abiotic components.

Activation of the three primary defoliation resistance mechanisms requires 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 processes in all parts of the plant; alters the plant community microclimate by changing light transmission, moisture relations, and temperature; and changes the soil environment, thereby affecting soil organism activity (Manske 2000a). Grass plants developed the defoliation resistance mechanisms in response to grazing during the period of coevoluation with graminivores (McNaughton 1979, 1983; Coleman et al. 1983; Briske 1991; Briske and Richards 1995; Manske 1999a, 2011b). The defoliation resistance mechanisms help grass tillers withstand and recover from partial defoliation by grazing. The three main resistance mechanisms are: compensatory internal physiological processes, internal vegetative production of secondary tillers from axillary buds, and external symbiotic rhizosphere organism activity (McNaughton 1979, 1983; Coleman et al. 1983; Ingham et al. 1985; Mueller and Richards 1986; Richards et al. 1988; Briske 1991; Murphy and Briske 1992; Briske and Richards 1994, 1995; Manske 1999a, 2011b).

Defoliation resistance mechanisms developed during the period of 30 to 20 mya as derivatives of the coevolution of grass plants, rhizosphere organisms, and large grazing mammalian graminivores following the cooling of the global climate in the Eocene that reduced forest ecosystems and increased grassland ecosystems. The defoliation resistance mechanisms are a complex assemblage of biogeochemical and physiological processes that involve intricate interactions among rhizosphere microorganisms, grass plants, and large grazing graminivores. Activation of these mechanisms provides important biological and physiological processes permitting native grasses to produce greater herbage biomass and to increase basal cover; these mechanisms also enable grass plants to replace lost leaf material, to restore disrupted physiological processes, and to vegetatively produce secondary tillers from axillary buds after partial defoliation by grazing. The defoliation resistance mechanisms function at variable levels of activation depending on the quantity of available mineral nitrogen in grassland ecosystem soil. When mineral nitrogen is available at 100 lbs/ac (112 kg/ha) or greater, the defoliation resistance mechanisms function at full activation (Manske 2011e). When mineral nitrogen is available at less than 100 lbs/ac (112 kg/ha), defoliation resistance mechanisms function at levels less than full activation (Manske 2009a, 2011d). In addition, the water (precipitation) use efficiency processes decrease in grass plants growing in ecosystems with less than 100 lbs/ac (112 kg/ha) available mineral nitrogen causing herbage biomass production to be reduced by 49.6% (Wight and Black 1972, 1979).

The quantity of available mineral nitrogen in grassland ecosystems is dependent on the rate of mineralization of soil organic nitrogen by rhizosphere organisms (Coleman et al. 1983). The larger the rhizosphere volume and microorganism biomass the greater the quantity of soil mineral nitrogen converted (Gorder, Manske, and Stroh 2004). Rhizosphere volume and microorganism biomass are limited by access to simple carbohydrate energy (Curl and Truelove 1986). Healthy grass plants capture and fix carbon during photosynthesis and produce carbohydrates in quantites greater than the amount needed for tiller growth and development (Coyne et al. 1995). Partial defoliation of grass tillers at vegetative phenological growth stages by large grazing graminivores causes greater quantities of exudates containing simple carbohydrates to be released from the grass tillers through the roots into the rhizosphere (Hamilton and Frank 2001). With the increase in availability of carbon compounds in the rhizosphere, the biomass and activity of the microorganisms increases (Anderson et al. 1981, Curl and Truelove 1986, Whipps 1990). The increase in rhizosphere organism biomass and activity results in greater rates of mineralization of soil organic nitrogen converting greater quantities of available mineral nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005). Mineral nitrogen available in quantities of 100 lbs/ac (112 kg/ha) or greater allow defoliated grass tillers full activation of the defoliation resistance mechanisms (Manske 2009a, 2011d, 2011e). Full activation of the compensatory internal physiological processes within grass plants accelerates growth rates of replacement leaves and shoots, increases photosynthetic capacity of remaining mature leaves, increases allocation of carbon and nitrogen, improves water (precipitation) use efficiency, and increases restoration of biological and physiological processes enabling rapid and complete recovery of partially defoliated grass tillers. Full activation of the asexual internal processes of vegetative production increases secondary tiller development from axillary buds and increases initiated tiller density during the grazing season. Full activation of the external symbiotic rhizosphere organism activity increases mineralization of mineral nitrogen, increases ecosystem biogeochemical cycling of essential elements, and improves belowground resource uptake competitiveness (Wight and Black 1972, 1979; McNaughton 1979, 1983; Coleman et al. 1983; Ingham et al. 1985; Mueller and Richards 1986; Richards et al. 1988; Briske 1991; Murphy and Briske 1992; Briske and Richards 1994, 1995; Manske 1999a, 2011b; Kochy and Wilson 2000).

Biogeochemical Processes

Biogeochemical processes are processes performed by soil microorganisms that renew the nutrient flow activities in ecosystem soils of renewable natural resources. Biogeochemical processes transform stored essential elements from organic forms into plant usable inorganic forms. Biogeochemical processes capture replacement quantities of lost or removed major essential elements of carbon, hydrogen, nitrogen, and oxygen with assistance from active live plants and transform the replacement essential elements into storage as organic forms for later use. Biogeochemical processes decompose complex unusable organic material into compounds and then into reusable essential elements. The quantity of biogeochemical processes conducted in renewable natural resource ecosystems determines the degree of ecosystem renewal and is dependant on the rhizosphere volume and soil microorganism biomass.

An evolutionary survival mechanism of grass plants in response to partial defoliation and the loss of leaf area as forage to grazing graminivores is the production of double the quantity of leaf biomass than needed for normal plant growth and maintenance (Crider 1955, Coyne et al. 1995). All of the aboveground herbage biomass produced by perennial grasses in a growing season represents about 33% of the total biomass produced. About 67% of the annual perennial grass biomass is produced belowground. About 50% of the aboveground biomass is expendable by the plant. About half of the expendable leaf material is removed as senescent leaves that are broken from the plant and fall to the ground as litter, or removed as leaf material consumed by wildlife or consumed and destroyed by grasshoppers and other insects. About half of the expendable leaf material, or 25% of the aboveground biomass is consumed by grazing livestock (Manske 2012b).

Perennial grass leaf material consists of digestible nutrients and nondigestible structural components. About 15% of the nutrients contained in the consumed leaf material is extracted by stocker heifers and steers and retained for growth. About

30% of the nutrients contained in the consumed leaf material is extracted by lactating cows, with a portion retained by the cow for production, and the remainder of the extracted nutrients passed to her calf for growth (Russelle 1992, Gibson 2009).

All of the nondigestible dry matter and most of the nutrients consumed by grazing graminivores are deposited on the ground as manure in a couple of days. Most of the nutrients consumed and used by graminivores for maintenance are returned to the ecosystem in the feces and urine. None of the herbage biomass dry matter produced during a growing season is removed by graminivores from the rangeland ecosystem. All of the essential elements contained in the belowground biomass and contained in the nonconsumed aboveground biomass stay in the ecosystem. Nearly all of the essential elements used in the annual production of herbage biomass and soil organism biomass are retained and recycled in the ecosystem. Recycling of retained ecosystem organic matter by soil microorganisms decomposes complex unusable material into compounds and then into reusable essential elements.

Some essential elements are lost or removed from the ecosystem as output. If the rangeland ecosystem is burned, almost all of the essential elements in the aboveground herbage are volatilized, and if the soil is dry, some of the belowground essential elements are also lost (Russelle 1992). The metabolic process of respiration in soil organisms, plants, livestock, wildlife, and grasshoppers results in a lose of some essential elements as carbon dioxide, water vapor, and heat energy. Some essential elements are removed from the ecosystem as weight biomass produced by wildlife and grasshoppers. The essential elements transferred from grass plants to grazing livestock and used for animal growth are removed from the ecosystem (Gibson 2009).

The small proportion of the ecosystem essential elements that are lost or removed annually need to be replenished by capturing input essential elements from the surrounding environment through ecosystem processes. The biogeochemical processes associated with active live plants and soil microorganisms can capture replacement quantities for the lost major essential elements of carbon, hydrogen, nitrogen, and oxygen.

Atmospheric carbon dioxide (CO_2) is the ecosystem input source for carbon. Atmospheric carbon dioxide which composes about 0.03% of the gasses in the atmosphere, exists at concentrations of around 370 to 385 mg/kg and is not limiting on rangelands. The carbon dioxide is fixed with hydrogen from soil water during the plant process of photosynthesis which converts energy from sunlight into chemical energy and assimilates simple carbohydrates. Capturing energy by fixing carbon has a relatively low impact on the plant organisms that posses chlorophyll and has low biological costs to the ecosystem resources (Manske 2011b).

Soil water (H_2O) is infiltrated precipitation water and is the ecosystem input source for hydrogen. Soil water is absorbed through the roots and distributed throughout the plant within the xylem vascular tissue. When the rate of water absorption by the roots is less than the rate of water loss from transpiration through stomata openings, plant tissue develops water stress (Brown 1995). Plant water stress limits growth. In western North Dakota, the perennial plant growing season months have a long-term periodicity rate of water deficiency conditions at 32.7%, for a mean of 2.0 months with water deficiency per growing season (Manske et al. 2010).

Wet deposition of nitrogen oxides (NO, N_2O) following lightning discharges is the ecosystem input source for nitrogen (Manske 2009b). The source of nitrogen for plant growth is mineral nitrogen (NO_3, NH_4) converted from soil organic nitrogen by rhizosphere organisms. Low quantities of available soil mineral nitrogen below 100 lbs/ac (112 kg/ha) is the major limiting factor of herbage growth on rangelands (Wight and Black 1979). However, rangeland soils are not deficient of nitrogen. Most of the nitrogen is immobilized in the soil as organic nitrogen. Soil organic nitrogen must be mineralized by rhizosphere organisms to become plant usable mineral nitrogen. The quantity of rhizosphere organisms is the limiting factor in rangeland ecosystems low in mineral nitrogen. Biomass and activity of organisms in the rhizosphere are limited by access to energy from simple carbohydrates which can be exudated from grass lead tillers with partial defoliation by grazing graminivores when grass tillers are at vegetative growth stages. Transforming nitrogen from organic nitrogen to mineral nitrogen and back to organic nitrogen is complex and has a great impact on many organisms at multiple trophic levels and has high biological costs on the ecosystem resources (Manske 2011a, 2011b).

Carbon dioxide, water, and nitrogen oxides are the ecosystem input sources for oxygen. Atmospheric oxygen composes about 28% of the gasses in the atmosphere. The oxygen cycle between the biotic and abiotic components of the ecosystem is closely linked to the carbon cycle and the water, or hydrological, cycle. Oxygen is vital for all organisms that carry out aerobic respiration. Oxygen is not limiting on rangeland ecosystems.

Radiant light from the sun is the ecosystem input source for energy. Radiant energy from the sun is necessary for photosynthesis (Manske 2011c). Intensity of sunlight can be greatly reduced by shading from taller plants. Nondefoliated live and standing dead leaves of grasses reduce light penetration to a similar degree as shrubs, even through shrub leaves are flat and wide and grass leaves are erect and linear (Kochy 1999). The light levels penetrating the leaf canopy can be about 20% of the light levels above the canopy (Peltzer and Kochy 2001).

Failure of a rangeland ecosystem to replenish essential elements at quantities equal to or greater than the annual amount of essential elements lost or removed from the ecosystem inhibits ecosystem biogeochemical processes from functioning at potential levels causing incremental decreases in productivity and gradual degradation of the ecosystem.

Ecosystem Dynamics

Native rangeland cool season grasses start early leaf greenup in mid April and grow slowly until early May, reaching 59% of the leaf growth in height by mid May. Most cool season grasses reach the three and a half new leaf stage around early June, reach 94% of the leaf growth in height by late June, and 100% of the leaf growth in height by late July. A few early developing cool season grasses start flower stalk development during mid May to early June. The other cool season grasses develop flower stalks during June. The needlegrasses start the flower stage during early June, with most cool season grasses starting to flower before 21 June. Flower stalks reach 94% of the growth in height by late June and 100% of the growth in height by late July when seeds are mature and being shed (Whitman et al. 1951, Goetz 1963, Manske 2000c).

The nutritional quality of ungrazed lead tillers of native rangeland cool season grasses changes with the tillers' phenological development. Early season growth stages during May have high crude protein levels above 16%. The early vegetative leaf stages contain levels of crude protein above 15% during early to mid June. As seed stalks begin to develop in early June, crude protein levels begin to decrease. At the flower stage, lead tillers contain 15% crude protein. After the flower stage and during the seed development stage, crude protein levels remain above 9.6% until mid July. As the ungrazed 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, Manske 2008a). Crude protein levels of grazing activated 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 2008a). Phosphorus levels of lead tillers drop below 0.18% in late July, when plants reach the mature seed stage (Whitman et al. 1951, Manske 2008b).

Native rangeland warm season grasses start early leaf greenup in mid May, reaching 44% of the leaf growth in height by early June, and most warm season grasses reach the three and a half new leaf stage around mid June. Warm season grasses reach 85% of the leaf growth in height by late June and reach 100% of the growth in height by late July. Flower stalk development starts during mid June, with the flower stage starting after 21 June. Most warm season grasses reach the flower stage by 15 July. The warm season flower stalks reach 91% of the growth in height by late July and reach 100% growth in height by late August when the seeds are mature and being shed (Whitman et al. 1951, Goetz 1963, Manske 2000c).

The nutritional quality of ungrazed lead tillers of native rangeland warm season grasses changes with the tillers' phenological development. Early season growth stages during May have high crude protein levels above 15%. The early vegetative leaf stages contain levels of crude above 13% during early to mid June. As seed stalks begin to develop in mid June, crude protein levels begin to decrease. At the flower stage, lead tillers contain 12.2% crude protein. After the flower stage and during the seed development stage, crude protein levels remain above 9.6% until late July. As the ungrazed 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% and below 6.0% in early September (Whitman et al. 1951, Manske 2008a). Crude protein levels of grazing activated warm season secondary tillers increase above 9.0% during August to 10.0% in early September, decrease during September, and drop below 9.6% in late September (Sedivec 1999, Manske 2008a). Phosphorus levels of lead tillers drop below 0.18%

in late August, when plants reach the mature seed stage (Whitman et al. 1951, Manske 2008b).

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. Premature grazing results in greatly reduced growth rates of herbage production (Coyne et al. 1995) causing decreased peak herbage biomass later in the growing season (Manske 2000b). Grazing that starts in mid to late May on native rangeland before the tillers reach the 3.5 new leaf stage results in a reduction of 45% to 60% from the potential herbage biomass that growing season (Campbell 1952, Rogler et al. 1962, Manske 2000b).

During the growing season, grass growth can be reduced by the environmental factors of inhibiting cool temperatures during the spring and fall and hot temperatures during the summer and by unevenly distributed precipitation. The precipitation received during the three month period, May, June, and July, is 50.7% of the annual precipitation, which is usually accompanied with generally low water deficiency conditions that reoccur with an average monthly rate during each of these three months at 20.6% of the growing seasons, and promotes rapid grass growth and development. Grass growth is limited during the three month period, August, September, and October, when the precipitation received is 25% of the annual amount and water deficiency conditions are usually high and reoccur with an average monthly rate during each of these three months at 49.7% of the growing seasons (Manske et al. 2010, Manske 2011f).

Low water infiltration on native rangelands and shallow soil water storage depths aggravate problems of grass plant growth between rain events. Restricted water infiltration increases the proportion of runoff precipitation, decreasing the quantity of water available for plant growth, and reducing the quantity of the effective precipitation. Low water infiltration rates and shallow water storage depths indicate inadequate soil aggregation and low soil fungi biomass. Aggregation of soil develops when an adequate biomass of soil fungi secrete large amounts of insoluable extracellular polysaccharids that have adhesive qualities (Caesar-TonThat and Cochran 2000; Caesar-TonThat et al. 2001a, 2001b; Caesar-TonThat 2002; Manske and Caesar-TonThat 2003). Aggregation of soil enlarges soil pore size, improves soil pore distribution, and stabilizes soil particles, resulting in improved water infiltration and increased soil water storage capacity (Caesar-TonThat et al. 2001b, Manske and Caesar-TonThat 2003). Greater soil aggregation increases the effectiveness of the precipitation received, increases the quantity of soil water available for plant growth, and reduces plant growth problems between rain events.

Water from precipitation is important for grass growth. However, herbage production in temperate rangelands is more often limited by deficiencies in mineral nitrogen than by water (Tilman 1990). Rangelands deficient in available soil mineral nitrogen produce less than potential quantities of herbage biomass (Wight and Black 1972). Native rangelands with a mineral nitrogen deficiency produce herbage weight per inch of precipitation received at 49.6% below the weight of herbage produced per inch of precipitation on rangeland without a mineral nitrogen deficiency (Wight and Black 1979).

Rangeland soils are not deficient of nitrogen. Most of the nitrogen is immobilized in the soil as organic nitrogen. Rangeland soils in the Northern Plains contain about 5 to 6 tons, with a range of 3 to 8 tons, of organic nitrogen per acre. The organic nitrogen is not available for plant use. Soil organic nitrogen must be converted into mineral nitrogen through mineralization by soil microorganisms. The quantity of soil organism biomass is the limiting factor in rangeland ecosystems low in mineral nitrogen. The rhizosphere soil organism biomass and activity are limited by access to short carbon chain energy. The primary producer trophic level in the rhizosphere are achlorophyllous saprophytes and can not fix carbon for energy. Greater quantities of carbon compound energy exudated into the rhizosphere increases the biomass and activity of the soil organisms resulting in increased mineralization of nitrogen, increased biogeochemical cycling of essential elements, and improvements of belowground resource competitiveness (Manske 1999a, 2011b). Mineral nitrogen available at 100 lbs/ac or greater is needed for herbage biomass weight to be produced at ecosystem potential levels (Wight and Black 1972).

The three month period, May, June, and July, is the period that receives the greatest amount of rainfall and is the short period of the growing season when grass lead tillers grow the most in height and weight. Cool season grasses develop to the 3.5 new leaf stage by early June and start the flower stage before 21 June. Warm season grasses develop to the 3.5 new leaf stage by mid June and reach the flower stage by mid July. Cool season grass lead tillers drop below 9.6% crude protein during the third week of July and warm season grass lead tillers drop below 9.6% crude protein during the fourth week of July (Manske 2000b, 2000c, 2008a). After mid to late July, native rangeland pastures managed with traditional concepts typically consists of herbage below the nutritional requirements of lactating beef cows. These cows lose body weight and decrease in daily milk production. The calves' average daily gain drops below 2.0 pounds per day (Manske 2002).

The herbage quality greatly declines on traditionally managed rangeland after July because little replacement leaf and shoot growth takes place and almost no new tiller growth occurs. Beef producers recognize the resulting decrease in cow and calf performance and usually try to compensate for the resulting reduced animal growth rates with nutrient supplementation. However, improvement of the nutritional quality of the herbage to meet the nutritional requirements of lactating beef cows during the latter portion of the grazing season until mid October can be accomplished by activation of the compensatory physiological processes within grazed grass plants that accelerate growth rates of replacement roots, leaves, and shoots, increases photosynthetic capacity of remaining mature leaves, increases allocation of carbon and nitrogen, improves water (precipitation) use efficiency, and increases restoration of biological processes enabling rapid and complete recovery of partially defoliated grass tillers, and by activation of the asexual processes of vegetative reproduction that increases secondary tiller development from axillary buds and increases tiller density during the growing season (Manske 1999a, 2011b). The resulting growth of replacement leaves and shoots and new secondary tillers from activation of the compensatory physiological processes and of the asexual processes of vegetative reproduction improves the nutritional quality of the available herbage during the latter portion of the grazing season above the nutrient requirements of lactating beef cows and supports animal weight performance at near genetic potentials (Manske 2002).

Almost every rangeland grass tiller grows during two growing seasons. The lead tillers that produced seed heads terminate at the end of the second growing season. Vegetative tillers that did not produce seed heads, activated secondary tillers, and fall initiated tillers that have grown during one growing season survive over the winter on stored carbohydrate reserves and grow again during the next growing season. The quantity of carbohydrates stored during the winter hardening process, that occurs from mid August to hard frost, is closely related to the amount of active leaf material on each tiller during that period. 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. Traditionally managed grazing of grass tillers during mid August to mid October that removes excessive leaf material from carryover tillers causes inadequate quantities of carbohydrates to be stored. Plants that have low carbohydrate reserves and survive the winter dormancy period produce tillers with reduced height and weight. Some of the tillers with low carbohydrate reserves deplete their stores through winter respiration before spring, causing winter kill of those tillers. Grazing native rangeland after mid October exacerbates these problems causing ecosystem degradation. The factors that reduce ecosystem productivity need not to occur.

Management of Native Rangelands

There are numerous factors that can negatively effect rangeland ecosystems and could cause reductions in productivity. Most of these negative factors have countermeasures that nullify or supersede the detrimental effects. During the period of 30 to 20 mya following global climate cooling, complex rangeland ecosystems developed as a result of the coevolution among modern native grasses, rhizosphere soil organisms, and large grazing mammalian graminivores. Numerous intricate interactive biological, physiological, and biogeochemical processes developed coincidentally with the coevolutionary creations. The primary processes are: internal compensatory physiological processes, internal asexual processes of vegetative reproduction, external symbiotic rhizosphere organism processes, and ecological biogeochemical processes. These critical processes permit rangeland ecosystems to function at potential levels. Unfortunately, these processes do not automatically function at full potential capacity. These processes require activation and they require adequate availability of carbon, hydrogen, nitrogen, and oxygen.

Native rangelands are optimally grazed by large graminivores as summer pastures from 1 June to mid October. Prior to early June, the cool season and warm season grasses are not physiologically capable of full recovery from grazing defoliation. After mid October, the nutritional quality of the herbage from the combination of lead tillers, vegetative tillers, and activated secondary tillers drops below the requirements of lactating beef cows.

Biologically effective management of native rangelands places first priority on meeting the biological and physiological requirements of the grass plants, soil organisms, and grazing animals, and to cycle the essential elements. The second priority is the diminishment of the factors that reduce ecosystem productivity and the enhancement of the factors that benefit ecosystem productivity. Perennial grass growth in the Northern Plains is restricted to a 6 month growing season, from mid April to mid October. Native rangeland grasses require 1.5 months of growth in the spring to reach grazing readyness resulting in a 4.5 month grazing season, from early June to mid October.

The twice-over rotation grazing management strategy is the biologically effective management practice that activates the beneficial defoliation resistance mechanisms and the biogeochemical processes. Partial defoliation controlled with the twice-over rotation grazing management strategy removes 25% to 33% of the leaf material from grass lead tillers at phenological growth between the three and a half new leaf stage and the flower (anthesis) stage during early June to mid July activates the beneficial processes. Full functionality of the defoliation resistance mechanisms requires mineral nitrogen to be available at 100 lbs/ac or greater and requires the quantity of available carbon fixed through photosynthesis from 75% to 67% of the leaf area of grass lead tillers prior to peak herbage biomass and from 50% of the leaf area post peak biomass (Manske 2010a, 2010b).

The twice-over rotation grazing management strategy uses three to six native rangeland pastures. Each of the pastures in the rotation is partially defoliated by grazing for 7 to 17 days during the first period, the 45 day interval from 1 June to 15 July when partial defoliation of grass lead tillers can activate the beneficial defoliation resistance mechanisms and biogeochemical processes. The length in number of days of the first grazing period on each pasture is the same percentage of 45 days as the percentage of the total season's grazable forage each pasture contributes to the complete system. The forage is measured as animal unit months (AUM's) of forage. The number of days grazed are not counted by calendar dates; days grazed are counted by the number of 24 hour periods grazed from the date and time the cattle are turned into a pasture. During the second grazing period, when lead tillers are maturing and defoliation by grazing is only moderately beneficial, the 90 day interval after mid July and before mid October, each pasture is grazed for double the number of days it was grazed during the first period. The pasture grazed first in the rotation sequence during one year is the last pasture grazed during the previous year (Manske 1999a, 2011b).

Management of native rangelands requires annual partial defoliation by large grazing graminivores managed by the biologically effective twice-over rotation strategy that coordinates defoliation events with grass phenological growth stages. The twice-over strategy activates the defoliation resistance mechanisms and the biogeochemical processes, and then maintains their functionality at potential levels. The twice-over strategy also meets the biological requirements of the grass plants and the rhizosphere organisms, and meets the nutritional requirements of the grazing animals during the entire grazing season. Biologically effective management of native rangeland ecosystems sustains healthy renewable natural resources that simultaneously provide greater forage for livestock, better habitat for prairie wildlife, more aesthetic prairie landscapes for recreation and sightseeing, increased food and fiber for people, and provides greater growing season residuum vegetation structure that is unfavorable habitat for pestiferous rangeland grasshopper population development.

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Literature Cited

Allen, E.B., and M.F. Allen. 1990. The mediation of competition by mycorrhizae in successional and patchy environments. p. 307-389. *in* J.B. Grace and D. Tilman (eds.). Perspectives on plant competition. Academic Press Inc., San Diego, CA.

Anderson, R.V., D.C. Coleman, C.V. Cole, and E.T. Elliott. 1981. Effect of nematodes *Acrobeloides sp.* and *Mesodiplogaster lheritieri* on substrate utilization and nitrogen and phosphorus mineralization. Ecology 62:549-555.

Beard, J.B. 1973. Turfgrass: science and culture. Prentice-Hall, Inc., Englewood Cliffs, NJ.

Belsky, A.J. 1992. Effects of grazing competition, disturbance and fire on species composition and diversity in grassland communities. Journal of Vegetation Science 3:187-200.

Bird, S.B., J.E. Herrick, M.M. Wander, and S.F. Wright. 2002. Spatial heterogeneity of aggregate stability and soil carbon in semi-arid rangeland. Environmental Pollution 116:445-455.

Box, J.E., and L.C. Hammond. 1990. Rhizosphere dynamics. Westview Press, Boulder, CO.

Branson, F.A. 1953. Two new factors affecting resistance of grasses to grazing. Journal of Range Management 6:165-171.

Briske, D.D. 1991. Developmental morphology and physiology of grasses. p. 85-108. *in* R.K. Heitschmidt and J.W. Stuth (eds.). Grazing management: an ecological perspective. Timber Press, Portland, OR.

Briske, D.D., and J.H. Richards. 1994. Physiological responses of individual plants to grazing: current status and ecological significance. p. 147-176. *in* M. Vavra, W.A. Laycock, and R.D. Pieper (eds.). Ecological implications of livestock herbivory in the west. Society for Range Management, Denver, CO.

Briske, D.D., and J.H. Richards. 1995. Plant response to defoliation: a physiological, morphological, and demographic evaluation. p. 635-710. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Brown, R.W. 1995. The water relations of range plants: adaptation of water deficits. p. 291-413. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and development morphology. Society for Range Mangement. Denver, CO.

Burrows, R.L., and F.L. Pfleger. 2002. Arbuscular mycorrhizal fungi respond to increasing plant diversity. Canadian Journal of Botany 80:120-130.

Butler, J.L., and D.D. Briske. 1988. Population structure and tiller demography of the bunch grass *Schizachyrium scoparium* in response to herbivory. Oikos 51:306-312.

Caesar-TonThat, T.C., and V. Cochran. 2000. Soil aggregate stabilization by a saprophytic lignin-decomposing basidiomycete fungus. I. Microbiological aspects. Biology and Fertility of Soils 32:374-380.

Caesar-TonThat, T.C., W. Shelver, R.G. Thorn, and V.L. Cochran. 2001a. Generation of antibodies for soil-aggregating basidiomycete detection to determine soil quality. Applied Soil Ecology 18:99-116.

Caesar-TonThat, T.C., D.H. Branson, J.D. Reeder, and L.L. Manske. 2001b. Soil-aggregating basidiomycetes in the rhizosphere of grasses under two grazing management systems. Poster. American Society of Agronomy Annual Meeting. Charlotte, NC.

Caesar-TonThat, T.C. 2002. Soil binding properties of mucilage produced by a basidiomycete fungus in a model system. Mycological Research 106:930-937.

Campbell, J.B. 1952. Farming range pastures. Journal of Range Management 5:252-258.

Campbell, R., and M.P. Greaves. 1990. Anatomy and community structure of the rhizosphere. p. 11-34. *in* J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

Chapman, G.P., and W.E. Peat. 1992. An introduction to the grasses. C.A.B. International, Wallingford, UK. 111p.

Chapman, G.P. 1996. The biology of grasses. C.A.B. International, Wallingford, UK. 273p.

Coleman, D.C., C.P.P. Reid, and C.V. Cole. 1983. Biological strategies of nutrient cycling in soil ecosystems. Advances in Ecological Research 13:1-55.

Coyne, P.I., M.J. Trlica, and C.E. Owensby. 1995. Carbon and nitrogen dynamics in range plants. p. 59-167. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Crider, F.J. 1955. Root-growth stoppage resulting from defoliation of grass. USDA Technical Bulletin 1102.

Curl, E.A., and B. Truelove. 1986. The rhizosphere. Springer-Verlag, New York, NY.

Dahl, B.E., and D.N. Hyder. 1977. Developmental morphology and management implications. p. 257-290. *in* R.E. Sosebee (ed.). Rangeland plant physiology. Range Science Series No. 4. Society for Range Management, Denver, CO.

Dahl, B.E. 1995. Developmental morphology of plants. p. 22-58. *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Driver, J.D., W.E. Holben, and M.C. Rillig. 2005. Characterization of glomalin as a hyphal wall component of arbuscular mycorrhizal fungi. Soil Biology and Biochemistry 37:101-106.

Elliot, E.T. 1978. Carbon, nitrogen and phosphorus transformations in gnotobiotic soil microcosms. M.S. Thesis. Colorado State University, Ft. Collins, CO.

Esau, K. 1960. Anatomy of seed plants. Wiley and Sons, New York, NY.

Evans, M.W., and F.O. Grover. 1940. Developmental morphology of the growing point of the shoot and the inflorescence in grasses. Journal of Agricultural Research 61:481-520.

Frank, A.B., J.D. Berdahl, and J.F. Karn. 1997. Phyllochron development in cool-season grasses. XVIII International Grassland Congress Poster.

Frank, A.B. 1996. Evaluating grass development for grazing management. Rangelands 18:106-109.

Gibson, D.J. 2009. Grasses and grassland ecology. Oxford University Press Inc., New York, NY. 305p.

Goetz, H. 1963. Growth and development of native range plants in the mixed prairie of western North Dakota. M. S. Thesis, North Dakota State University, Fargo, ND. 165p.

Gorder, M.M., L.L. Manske, and T.L. Stroh. 2004. Grazing treatment effects on vegetative tillering and soil rhizospheres of western wheatgrass. NDSU Dickinson Research Extension Center. Range Research Report DREC 04-1056. Dickinson, ND. 13p.

Hamilton, E.W., and D.A. Frank. 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82:2397-2402.

Harley, J.L., and S.E. Smith. 1983. Mycorrhizal symbiosis. Academic Press, New York, NY.

Hyder, D.N. 1974. Morphogenesis and management of perennial grasses in the U.S. p. 89-98. *in* Plant morphogenesis as the basis for scientific management for range resources. USDA Miscellaneous Publication 1271.

Ingham, R.E., J.A. Trofymow, E.R. Ingham, and D.C. Coleman. 1985. Interactions of bacteria, fungi, and the nemotode grazers: effects of nutrient cycling and plant growth. Ecological Monographs 55:119-140.

Klein, D.A., B.A. Frederick, M. Biondini, and M.J. Trlica. 1988. Rhizosphere microorganism effects on soluble amino acids, sugars, and organic acids in the root zone of *Agropyron cristatum, A. smithii,* and *Bouteloua gracilis*. Plant and Soil 110:19-25.

Kochy, M., and S.D. Wilson. 2000. Competitive effects of shrubs and grasses in prairie. Oikos 91:385-395.

Kochy, M. 1999. Grass-tree interactions in western Canada. Ph.D. Dissertation. University of Regina. Regina, Saskatchewan, Canada.

Koide, R.T. 1993. Physiology of the mycorrhizal plant. p. 33-54. *in* D.S. Ingram and P.H. Williams (eds.). Mycorrhiza synthesis. Academic Press, London, UK.

Langer, R.H.M. 1956. Growth and nutrition of timothy (*Phleum pratense).* I. The life history of individual tillers. Annals of Applied Biology 44:166-187.

Langer, R.H.M. 1963. Tillering in herbage grasses. Herbage Abstracts 33:141-148.

Langer, R.H.M. 1972. How grasses grow. Edward Arnold, London, Great Britain.

Leopold, A.C., and P.E. Kriedemann. 1975. Plant growth and development. McGraw-Hill Book Co., New York, NY.

Manske, L.L. and T.C. Caesar-TonThat. 2003. Increasing rhizosphere fungi and improving soil quality with biologically effective grazing management. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 03-3025. Dickinson, ND. 6p.

Manske, L.L., S. Schneider, J.A. Urban, and J.J. Kubik. 2010. Plant water stress frequency and periodicity in western North Dakota. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1077. Dickinson, ND. 11p.

Manske, L.L. 1996a. Adaptive tolerance mechanisms in grass plants. p. 97-99. *in Z.* Abouguendia (ed.). Total ranch management in the Northern Great Plains. Grazing and Pasture Technology Program, Saskatchewan Agriculture and Food. Regina, Saskatchewan, Canada.

Manske, L.L. 1999a. Can native prairie be sustained under livestock grazing? Provincial Museum of Alberta. Natural History Occasional Paper No. 24. Edmonton, Alberta. p.99-108.

Manske, L.L. 2000a. Management of Northern Great Plains prairie based on biological requirements of the plants. NDSU Dickinson Research Extension Center. Range Science Report DREC 00-1028. Dickinson, ND. 12p.

Manske, L.L. 2000b. Grazing before grass is ready. NDSU Dickinson Research Extension Center. Range Management Report DREC 00-1032. Dickinson, ND. 6p.

Manske, L.L. 2000c. Grass growth in height. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 00-3020. Dickinson, ND. 4p.

Manske, L.L. 2002. Evaluation of twelve-month pasture-forage management strategies for range cows. NDSU Dickinson Research Extension Center. Rangeland Research Extension Program DREC 02-4004. Dickinson, ND. 147p.

Manske, L.L. 2007. Ectomycorrhizal Basidiomycete fungi detected in rhizospheres of mixed grass prairie grasses. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 07-3047. Dickinson, ND. 3p.

Manske, L.L. 2008a. Annual nutritional quality curves for graminoids in the Northern Plains. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 08-3014c. Dickinson, ND. 15p.

Manske, L.L. 2008b. Annual mineral quality curves for graminoids in the Northern Plains. NDSU Dickinson Research Extension Center. Range Management Report DREC 08-1030b. Dickinson, ND. 15p.

Manske, L.L. 2009a. Grass plant responses to defoliation. NDSU Dickinson Research Extension Center. Range Research Report DREC 09-1074. Dickinson, ND. 47p.

Manske, L.L. 2009b. Enhancement of the nitrogen cycle improves native rangeland. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 09-3054. Dickinson, ND. 6p.

Manske, L.L. 2010a. Leaf stage development of western wheatgrass tillers. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1075. Dickinson, ND. 48p.

Manske, L.L. 2010b. Evaluation of the defoliation resistance mechanisms influence on vegetative tiller initiation and tiller density. NDSU Dickinson Research Extension Center. Range Research Report DREC 10-1076. Dickinson, ND. 13p.

Manske, L.L. 2011a. Grazing and burning treatment effects on soil mineral nitrogen and rhizosphere volume. NDSU Dickinson Research Extension Center. Range Research Report DREC 11-1066c. Dickinson, ND. 15p.

Manske, L.L. 2011b. Biology of defoliation by grazing. NDSU Dickinson Research Extension Center. Range Management Report DREC 11-1067b. Dickinson, ND. 25p.

Manske, L.L. 2011c. Range plant growth and development are affected by climatic factors. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 11-3019c. Dickinson, ND. 5p.

Manske, L.L. 2011d. Biologically effective grazing management reduces the detrimental effects from drought conditions on grasslands. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 11-3049b. Dickinson, ND. 6p.

Manske, L.L. 2011e. Soil mineral nitrogen increased above the threshold quantity of 100 pounds per acre in rangeland ecosystems. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 11-3056. Dickinson, ND. 8p.

Manske, L.L. 2011f. Environmental factors to consider during planning of management for range plants in the Dickinson, North Dakota, region, 1892-2010. NDSU Dickinson Research Extension Center. Range Research Report DREC 11-1018n. Dickinson, North Dakota. 40 p.

Manske, L.L. 2012b. Degradation and biological restoration of mixed grass prairie ecosystems. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 12-3058. Dickinson, ND. 16p.

Marschner, H., and B. Dell. 1994. Nutrient uptake in mycorrhizal symbiosis. Plant and Soil 159:89-102.

Marschner, H. 1992. Nutrient dynamics at the soil-root interface (Rhizosphere). p. 3-12. *in* D.J. Read, D.H. Lewis, A.H. Fitter, and I.J. Alexander (eds.). Mycorrhizas in ecosystems. C.A.B. International, Wallingford, U.K.

McMillan, C. 1957. Nature of the plant community. III. Flowering behavior within two grassland communities under reciprocal transplanting. American Journal of Botany 44:144-153.

McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist 113:691-703.

McNaughton, S.J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329-336.

Millard, P., R.J. Thomas, and S.T. Buckland. 1990. Nitrogen supply affects the remobilization of nitrogen for the growth of defoliation *Lolium perenne* L.J. Experimental Botany 41:941-947.

Moorman, T., and F.B. Reeves. 1979. The role of endomycorrhizae in revegetation practices in the semi-arid west. II. A bioassay to determine the effect of land disturbance on endomycorrhizal populations. American Journal of Botany 66:14-18.

Moser, L.E. 1977. Carbohydrate translocation in range plants. p. 47-71 *in* R.E. Sosebee (ed.). Rangeland plant physiology. Range Science Series No. 4. Society for Range Management, Denver, CO.

Mueller, R.J., and J.H. Richards. 1986. Morphological analysis of tillering in *Agropyron spicatum* and *Agropyron desertorum.* Annals of Botany 58:911-921.

Murphy, J.S., and D.D. Briske. 1992. Regulation of tillering by apical dominance: chronology, interpretive value, and current perspectives. Journal of Range Management 45:419-429.

Ourry, A., J. Boucaud, and J. Salette. 1990. Partitioning and remobilization of nitrogen during regrowth in nitrogen-deficient ryegrass. Crop Science 30:1251-1254.

Peltzer, D.A., and M. Kochy. 2001. Competitive effects of grasses and woody plants in mixed grass prairie. Journal of Ecology 89:519-527.

Rechenthin, C.A. 1956. Elementary morphology of grass growth and how it affects utilization. Journal of Range Management 9:167-170.

Richards, J.H., and M.M. Caldwell. 1985. Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: a field study with *Agropyron* species. Journal of Applied Ecology 22:907-920.

Richards, J.H., R.J. Mueller, and J.J. Mott. 1988. Tillering in tussock grasses in relation to defoliation and apical bud removal. Annals of Botany 62:173-179.

Rillig, M.C., S.F. Wright, and V.T. Eviner. 2002. The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. Plant and Soil 238:325-333.

Roberts, R.M. 1939. Further studies of the effects of temperature and other environmental factors upon the photoperiodic response of plants. Journal of Agricultural Research 59:699-709.

Rogler, G.A., R.J. Lorenz, and H.M. Schaaf. 1962. Progress with grass. North Dakota Agricultural Experiment Station. Bulletin 439. 15p.

Russelle, M.P. 1992. Nitrogen cycling in pastures and range. Journal of Production Agriculture 5:13-23.

Ryle, G.J., and C.E. Powell. 1975. Defoliation and regrowth in the graminaceous plant: the role of current assimilate. Annals of Botany 39:297-310.

Sedivec, K. 1999. Nutritional quality of selected rangeland plants. Summary Report. NDSU Animal and Range Sciences Department. Research Report. Fargo, ND.

Smith, S.E., and D.J. Read. 1997. Mycorrhizal symbiosis. Academic Press, San Diego, CA.

Tilman, D. 1990. Constraints and Tradeoffs: toward a predictive theory of competition and succession. Oikos 58:3-15.

Weier, T.E., C.R. Stocking, and M.G. Barbour. 1974. Botany: an introduction to plant biology. John Wiley and Sons, New York, NY.

Whipps, J.M. 1990. Carbon economy. p. 59-97. *in* J.M. Lynch (ed.). The rhizosphere. John Wiley and Sons, New York, NY.

Whitman, W.C., D.W. Bolin, E.W. Klosterman, H.J. Klostermann, K.D. Ford, L. Moomaw, D.G. Hoag, and M.L. Buchanan. 1951. Carotene, protein, and phosphorus in range and tame grasses of western North Dakota. North Dakota Agricultural Experiment Station. Bulletin 370. Fargo, ND. 55p.

Wight, J.R., and A.L. Black. 1972. Energy fixation and precipitation use efficiency in a fertilized rangeland ecosystem of the Northern Great Plains. Journal of Range Management 25:376-380.

Wight, J.R., and A.L. Black. 1979. Range fertilization: plant response and water use. Journal of Range Management 32:345-349.

Wilson, A.M., and D.D. Briske. 1979. Seminal and adventitious root growth of blue grama seedlings on the central plains. Journal of Range Management 32:209-213.