

Biogeochemical Processes of Nitrogen in Rangeland Soils

Llewellyn L. Manske PhD
Research Professor of Range Science
North Dakota State University
Dickinson Research Extension Center
Report DREC 15-3066

Native rangelands of the Northern Plains are deficient in available soil mineral nitrogen (Power and Alessi 1971; Wight and Black 1972, 1979; Goetz 1984; Tilman 1990). The widespread deficient quantities of mineral nitrogen in the soils of mixed grass prairie pastures is the major cause for grass herbage production and calf weight gains to be at less than potential levels.

Wight and Black (1972,1979) evaluated herbage yield, plant species composition, and precipitation (water) use efficiency of mixed grass prairie at various quantities of available soil mineral nitrogen over a ten year period that had average annual precipitation at 13% above the long-term mean. They concluded that nitrogen was a major growth limiting factor in the Northern Plains, that increasing herbage biomass production to biological potential levels on rangeland ecosystems would require sustained mineralization rates that supplied 100 to 165 pounds of available mineral nitrogen per acre per year, and that 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 by 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 had no mineral nitrogen deficiencies.

Manske (2012a) documented quantities of available mineral nitrogen that ranged from 31.2 lbs/ac to 76.7 lbs/ac on five traditional management treatments with operational histories of 20 to 75 years. These low quantities of available mineral nitrogen that are well below the threshold level of 100 lbs/ac indicate that long-term traditional grazing management and long-term nongrazing practices result in rangeland ecosystems with considerable inhibitory mineral nitrogen deficiencies (table 1).

The symptoms of low herbage biomass production, deterioration of plant density and species composition, and reduced livestock weight performance caused by deficient quantities of mineral nitrogen in pasture soils are easily observable.

Livestock producers typically treat these symptoms with costly practices of feeding creep to the calves and providing supplemental crude protein to the cows. Supplemental amendments of nitrogen through agronomic practices of fertilization and alfalfa interseeding have been typically used to increase soil mineral nitrogen. Extensive research has found that these agronomic practices are not successful solutions and that they actually cause additional long lasting problems (Manske et al. 2005, 2014c). Treating the symptoms has not corrected the problems.

Deficiencies of soil mineral nitrogen in rangeland soils are not the result of low quantities of nitrogen. About 78% of the atmospheric volume consists of dinitrogen gas (N_2). The column of air above an acre of land contains about 34,500 tons of dinitrogen gas (Foth 1978). Dinitrogen gas in the atmosphere is not directly available to higher plants. Atmospheric dinitrogen can be fixed by a few types of bacteria and by lightning and then moved into the soil. Lightning discharges combine dinitrogen (N_2) and oxygen (O_2) to produce nitric acid (NO) and dinitrogen oxide (N_2O) that are deposited on the land in precipitation at a rate around 5 to 6 pounds per acre per year in temperate regions (Brady 1974, Gibson 2009). Gaseous nitrogen oxides [nitric acid (NO) and dinitrogen oxide (N_2O)] and ammonia (NH_3) occur in the atmosphere and can be absorbed directly by leaves of higher plants through stomata (Coyne et al. 1995) and are eventually moved into the soil.

Rangeland soils of the Northern Plains have been accumulating nitrogen at a few pounds per acre per year for about 5000 years since the current climate started (Bluemle 2000, Manske 2008). Most prairie soils contain 5 to 6 tons of nitrogen per acre. The nitrogen in rangeland soils is primarily in the organic form and not available to plants. A very large portion of the soil organic nitrogen is contained in the soil organic matter detritus at various stages of physical breakdown and decomposition (Legg 1975). Some of the organic nitrogen is immobilized in living tissue of plants, microorganisms, and animals as essential constituents of proteins and nucleotides. A small amount of the soil nitrogen is in the mineral

form as ammonium (NH_4) and nitrate (NO_3) with an immeasurably minute amount as nitrate (NO_2). Annually, the amount of nitrogen entering a prairie ecosystem through wet and dry deposition or leaving an ecosystem as livestock weight is exceedingly small compared with the amounts held as organic forms in plants and microbes or in soil organic matter (Coyne et al. 1995).

Rangelands of the Northern Plains are not inherently low producing ecosystems. Typical low grass herbage production and calf weight gains on rangeland pastures that result from deficient quantities of available soil mineral nitrogen is strictly a management caused problem. Development of management solutions requires a working knowledge of the biogeochemical processes of nitrogen in rangeland ecosystems.

Biogeochemical Processes

The nitrogen cycle within rangeland soils functions around two major biogeochemical processes: immobilization and mineralization. These processes take place simultaneously with plant growth, dieback, and microbial decomposition (Legg 1975). Immobilization is the process of assimilation of mineral nitrogen into organic forms of living organisms. Mineralization is the process of converting organic nitrogen into mineral (inorganic) nitrogen. The quantity of mineral nitrogen in a soil is the net difference between the total quantity of organic nitrogen mineralized by soil microorganisms and the quantity of mineral nitrogen immobilized by plants and soil microbes (Brady 1974, Legg 1975).

Immobilization of nitrogen is a biological process by which plants and soil microorganisms can assimilate absorbed inorganic nitrogen into essential organic nitrogen compounds. Ammonium (NH_4) and nitrate (NO_3) are the two most important forms of available mineral nitrogen in soils and both are readily absorbed by grassland plant roots and soil microorganisms. At low temperatures, ammonium uptake is greater than nitrate uptake (Coyne et al. 1995).

Nitrogen uptake of both ammonium and nitrate directly into grassland plant roots requires energy and takes place during the daytime while plants are conducting photosynthesis and a source of energy is readily available (Coyne et al. 1995). In prairie soils where ammonium is the major nitrogen source, mycorrhizal symbiotic fungi enhance nitrogen uptake and reduce the energy cost to host plants (Coyne et al. 1995). Endomycorrhizal fungi can

absorb both ammonia (NH_3) and ammonium (NH_4) and pass these nitrogen forms directly into the host plant, or the fungi can nitrify these forms of nitrogen into nitrate (NO_3) and then transport it into the roots of the host plant (Moorman and Reeves 1979, Harley and Smith 1983, Allen and Allen 1990, Box and Hammond 1990, Marschner 1992, Manske 1996).

Absorbed ammonium must have immediate assimilation with carbon upon entering root tissue and then be converted into amino acids (Coyne et al. 1995). Absorbed nitrates can be reduced to ammonia or ammonium and then converted to amino acids in the roots, transported to the shoots or leaves for assimilation into amino acids or stored in cell vacuoles for later use (Coyne et al. 1995). The greatest quantity of nitrate use occurs during the vegetative growth stage until just past the flower stage (Brady 1974).

The recently formed amino acids can be used immediately to build complex nitrogenous compounds, or the amino acids can float around inside the plant for later use (Coyne et al. 1995). Amino acids are building blocks for proteins, nucleotides, and chlorophyll. Proteins are used to form enzymes, hormones, and structural components of cells. Nucleotides build nucleic acids, deoxyribonucleic acid (DNA) and ribonucleic acid (RNA), that are the genetic material that control all cellular functions and heredity (Coyne et al. 1995). About half of the organic nitrogen is in the form of amino compounds (Brady 1974).

The nitrogen assimilated into complex organic compounds is immobilized and thus protected from loss by leaching or volatilization (Legg 1975, Gibson 2009). Organic nitrogen is tied up in living tissue and in soil organic matter for three to four years in northern rangeland soils (Power 1972) and is unavailable for use by higher plants until after it has been mineralized by soil microorganisms.

Mineralization is a complex biogeochemical process conducted by a large number of saprotrophic and heterotrophic soil microorganisms that convert immobilized organic nitrogen from soil organic matter detritus and from living tissue of plant roots or other soil microbes into mineral (inorganic) nitrogen (Power 1972). Ammonium salts are the first inorganic nitrogen compounds produced by microbial digestion. 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

(NH₃) and carbon dioxide, or other low molecular weight carbon compounds (Power 1972, Brady 1974). Most of the ammonia released into soil water is readily hydrolyzed into stable ammonium (NH₄).

The ammonium ions (NH₄⁺) are fairly immobile but have several optional biological and chemical pathways; the cations can be absorbed directly by plant roots, absorbed by soil microbes or symbiotic fungi, adsorbed to clay lattice structure, attached to organic matter or mineral soil, or be oxidized during nitrification producing nitrite (NO₂) and then nitrate (NO₃) (Brady 1974, Legg 1975, Coyne et al. 1995).

The nitrate ions (NO₃⁻) are repelled by soil particles and considered to be mobile moving freely in the soil with water (Coyne et al. 1995). The quantity of available nitrate in soil increases when the soil moisture content increases (Brady 1974).

Some forms of mineral nitrogen are fairly active and can be lost from the soil. In dry soils low in hydrogen ions, some of the gaseous ammonia (NH₃) near the soil surface that has not been hydrolyzed are volatilized into the atmosphere. In mesic regions where soil water can move below the rooting depth, some of the nitrate (NO₃) in solution can be lost by leaching (Legg 1975, Gibson 2009). However, none of the mineral nitrogen in the Northern Plains 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 the arid and semiarid regions of the short grass and mixed grass prairies that are covered with perennial vegetation (Brady 1974, Wight and Black 1979). Leaching losses of mineral nitrogen in the sub humid and humid regions of the mixed grass and tall grass prairies are negligible (Brady 1974, Coyne et al. 1995).

Burning of rangelands by prescribed fire and wild fire causes volatilization of the nitrogen contained in the aboveground herbage and litter. Combustion causes nitrogen losses approaching 90% primarily as ammonia (NH₃), dinitrogen oxide (N₂O), and other nitrogen oxides (Russelle 1992). Little belowground nitrogen is volatilized when soil is moist during the burn, however, when 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.

The quantity of available ammonium in grassland ecosystems is dependant on the rate of mineralization of soil organic nitrogen (Coleman et al. 1983). The mineralization rate is determined by the microorganism biomass, and the microorganism biomass is limited by access to simple carbohydrate energy (Curl and Truelove 1986).

The available energy from soil organic matter is inadequate to increase soil microorganism biomass substantially. Soil organic matter (SOM) contains energy at a rate of about 4-5 kilocalories/gram which would translate into nearly 200 million kilocalories of energy in the top six inches of an acre of soil (Brady 1974). Most of this energy is lost during microbial decomposition and dissipated from the soil as heat. The small amount of energy available to soil organisms in fresh organic material comes from short chain carbohydrates of sugars and starches (1-5%) and from water soluble proteins (very low %) (Brady 1974).

Manipulation of the mineralization rates with grazing management will require increases in available energy from plant sources in order to increase the soil microorganism biomass. Grassland plants exude substances through the roots into the surrounding soil. Root exudates include sugars, amino acids, proteins, and numerous carbon compounds (Coyne et al. 1995). The quantity of exudates differ with plant species and is variable with phenological growth stage. The quantity of root exudate leakage from ungrazed grassland plants support only a small microorganism biomass that are capable of mineralizing low amounts of mineral nitrogen (Manske 2012b). Rangeland ecosystems require a minimum of 100 lbs/ac of available mineral nitrogen to produce herbage biomass at the biological potential rates (Wight and Black 1972).

Partial defoliation of grass tillers at vegetative phenological growth stages by large grazing graminivores causes greater quantities of exudates containing simple carbohydrate energy to be released from the grass tillers through the roots into the rhizosphere (Hamilton and Frank 2001, Manske 2011a). With the increase in availability of energy from 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 transforming into 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). Increasing available mineral nitrogen in rangeland soils with grazing management strategies will require the participation of large grazing graminivores, grass plants, and rhizosphere microorganisms and the activation of the defoliation resistance mechanisms.

Defoliation Resistance Mechanisms

Grassland ecosystems developed as a result of the global climate cooling near the end of the Eocene epoch around 34 mya that reduced the forest ecosystems to open savannah ecosystems then to grassland ecosystems (Chintauan-Marquier et al. 2011, Gomez et al. 2012, Anissimov 2013, Anonymous 2013). During the period of 30 to 20 mya, modern native grasses, rhizosphere microorganisms, and large grazing mammalian graminivores, coevolved and developed complex interactive processes that improved mutual survival of the organisms and perpetuation of the grassland ecosystems.

The complex interrelationships among grass plants, soil microbes, and graminivores are symbiotic. 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, dead plant material, and soil microbe remains. Rhizosphere organisms depend on grass plants for energy in the form of short carbon chains. Grass plants exude short carbon chain energy through the roots into the rhizosphere following partial defoliation by grazing graminivores of the aboveground leaf material at vegetative phenological growth stages. Grass plants produce double the leaf biomass than is needed by the plant in order to provide nutritious leaf forage for grazing graminivores.

The complex interactions that occur in grassland ecosystems that help grass tillers withstand and recover from partial defoliation by grazing are the defoliation resistance mechanisms (McNaughton 1979, 1983; Briske 1991; Briske and Richards 1994, 1995; Manske 1999). The three primary mechanisms are: compensatory internal physiological processes (McNaughton 1979, 1983; Briske 1991); asexual internal processes of vegetative tiller production (Mueller and Richards 1986, Richards et al. 1988, Murphy and Briske 1992, Briske and Richards 1994, 1995); and external symbiotic rhizosphere organism activity (Coleman et al. 1983, Ingham et al. 1985). These processes have been reviewed and described

by Manske (2011b) and are summarized in the following paragraphs.

The compensatory internal physiological processes increase the restoration of biological and physiological processes enabling rapid and complete recovery of plant biomass in partially defoliated grass tillers (Langer 1972, Briske and Richards 1995). The growth rates of replacement leaves and shoots increase producing larger leaves with greater mass (Langer 1972, Briske and Richards 1995). Photosynthetic capacity increases in remaining mature leaves and rejuvenated portions of older leaves not completely senescent (Atkinson 1986, Briske and Richards 1995). Allocation of the carbon recently fixed by photosynthesis in remaining rejuvenated mature leaves and the nitrogen recently mineralized from soil organic nitrogen by active rhizosphere organisms increases and moved to active growing points (Richards and Caldwell 1985, Briske and Richards 1995, Coyne et al. 1995). Water (precipitation) use efficiency with increased herbage biomass production improves (Smika et al. 1965; Wight and Black 1972, 1979; Whitman 1976, 1978).

Asexual internal processes of vegetative tiller development from axillary buds is the dominant form of reproduction in semiarid and mesic grasslands (short grass, mixed grass, and tall grass prairies) (Belsky 1992, Chapman and Peat 1992, Briske and Richards 1995, Chapman 1996, Manske 1999) not sexual reproduction and the development of seedlings. Secondary tiller development from axillary buds increases (Moser 1977, Dahl and Hyder 1977, Dahl 1995). Initiated tiller density increases with the suppression of the inhibiting hormone, auxin (Murphy and Briske 1992, Briske and Richards 1994, 1995).

External symbiotic rhizosphere organism activity is absolutely necessary for the recycling of the essential elements (Coleman et al. 1983, Ingham et al. 1985). Mineralization of essential elements increases (Coleman et al. 1983, Klein et al. 1988); the macronutrients, nitrogen (N), phosphorus (P), and sulfur (S) are in the form of organic compounds in soil organic matter and are mineralized by soil microbes, and potassium (K), calcium (Ca), and magnesium (Mg) are inorganic cations adsorbed to organic particles in soil organic matter. Ecosystem biogeochemical cycling of essential elements, carbon (C), hydrogen (H), oxygen (O), and the micronutrients, renews the nutrient flow activities in ecosystem soils (Coleman et al. 1983, Klein et al. 1988). Belowground resource uptake competitiveness of grass plants improves (Li and

Wilson 1998, Kochy 1999, Kochy and Wilson 2000, Peltzer and Kochy 2001).

Activation of the Defoliation Resistance Mechanisms

Activation of the defoliation resistance mechanisms requires a complex assemblage of biogeochemical processes that involve intricate interactions among grass plants, rhizosphere microorganisms, and large grazing graminivores (Manske 1999)

Healthy grass plants capture and fix carbon from atmospheric carbon dioxide during photosynthesis that combines carbon, hydrogen, and oxygen to produce carbohydrates in quantities greater than the amount needed for tiller growth and development (Coyne et al. 1995). The surplus short chain carbon compounds are available to supply the energy needed by the rhizosphere microorganisms. The only time in which the surplus carbon energy can be moved from the grass tiller through the roots into the rhizosphere is while a tiller is in the vegetative growth stage. During vegetative growth, the aboveground foliage consists primarily of crude protein (nitrogen) and water; most of the carbon is still in the belowground parts. Partial defoliation of the aboveground vegetative leaves removes more nitrogen than carbon from the plant and disrupts the tillers C: N ratio forcing that tiller to release (exudate) some of its carbon into the rhizosphere.

Partial defoliation of tillers before the third new leaf stage, when the plants are low in carbohydrates, results in reduced growth rates of herbage production for the remainder of the growing season (Campbell 1952, Rogler et al. 1962, Manske 2000b) because the amount of photosynthetic product synthesized by the small leaf area of remaining early growth leaves is insufficient to meet the requirements for new leaf growth (Heady 1975, Coyne et al. 1995, Manske 1994, 2000b). After the tiller has produced three and half new leaves, the leaf area is large enough to synthesize photosynthate at sufficient quantities to meet leaf growth requirements (Manske 2011b).

Almost all grass tillers live for two growing seasons, tillers produce vegetative growth during the first growing season and during the second growing season, the lead tillers develop flower stalks (Manske 2014a). As the vegetative leaves mature, complex structural carbon compounds, cellulose and hemicellulose, increase and lignin forms in the cell walls (Manske 2011b). Partial defoliation after mid

July no longer disrupts the C: N ratio and carbon energy is not forced out of the grass tillers into the rhizosphere. The period during which the defoliation resistance mechanism can be activated with partial defoliation by large grazing graminivores that causes surplus carbon energy to be moved from the tiller into the rhizosphere is short; for cool and warm season native grasses, the combined time is 45 days from 1 June to 15 July (the 3.5 new leaf stage to the flower stage), and for the major domesticated cool season grasses, the time is 40 days from 1 May to 10 June (also the 3.5 new leaf stage to the flower stage) (Manske 2011b).

Maintaining functionality of the activated mechanisms has a high carbon and nitrogen demand at the increased quantity of active growing points. The source of the carbon is preferentially allocated from the carbon recently fixed by photosynthesis in the remaining rejuvenated older leaves and the source of the nitrogen is preferentially allocated from the nitrogen recently mineralized from soil organic nitrogen by rhizosphere microorganisms (Ryle and Powell 1975, Richards and Caldwell 1985, Briske and Richards 1995). The variable quantities of available mineral nitrogen and carbon that can be used for rapid restoration of lost plant biomass regulates the variable levels of performance of the defoliation resistance mechanisms (Manske 2010b).

Wight and Black (1972, 1979) found that a minimum threshold quantity of 100 lbs/ac of available mineral nitrogen was required to fully activate the water (precipitation) use efficiency processes that enable a sustained herbage biomass production at biological potential levels on mixed grass prairie. Rangelands that have less than 100 lbs/ac mineral nitrogen have nitrogen deficiencies that cause the weight of herbage production per inch of precipitation received to be reduced an average of 49.6%. Mineralization at high rates that supply mineral nitrogen at 100 lbs/ac can not be obtained from traditional grazing practices (Wight and Black 1972, Manske 2012a, table 1).

Manske (2010a, 2010b) found that partial defoliation by large grazing graminivores 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 and activated the asexual processes of vegetative tiller production on rangeland pastures that had 100 lbs/ac or greater of available mineral nitrogen. However, this same defoliation treatment did not activate the defoliation resistance mechanisms of grass plants on rangeland ecosystems

that had soil mineral nitrogen available at quantities of less than 100 lbs/ac.

The defoliation resistance mechanisms do not function automatically; they require annual activation by partial defoliation of tillers at the vegetative growth stages between the three and a half new leaf stage and the flower stage; and the mechanisms do not function unless 100 lbs/ac of mineral nitrogen is available from the rhizosphere microorganisms (Wight and Black 1972, 1979, Manske 2010a, 2010b, 2014a, 2014b). Activation of the defoliation resistance mechanisms requires that the rhizosphere microbe biomass be increased to the level that is capable of mineralizing nitrogen at a high rate of 100 lbs/ac or greater. Rangelands in typical condition that have had a history of management of strong land stewardship ethics with traditional grazing practices requires two to three growing seasons to increase the soil microbe biomass; rangelands in poorer condition require five to seven years; and rangelands with histories of winter grazing or nongrazing require more than ten years to increase the soil microbe biomass sufficiently (Manske 2011b, 2012b).

Crider (1955) conducted an extensive study that found that grass tillers with 50% or more of the aboveground leaf material removed reduce root growth, root respiration, and root nutrient absorption. These physiological functions of grass plants have recently been described as the process of “belowground resource uptake competitiveness” that were documented by Kochoy and Wilson (2000). Crider’s work led to the familiar range axiom “take half and leave half” which is still sound advice for grazing periods after peak herbage biomass has been reached during the last two weeks of July (Manske 2000a).

Removal of 50% of the leaf weight of vegetative grass tillers between the 3.5 new leaf stage and the flower stage did not activate the compensatory physiological processes nor the asexual processes of vegetative production of tillers from axillary buds regardless of whether the available mineral nitrogen was above or below the threshold of 100 lbs/ac. The remaining 50% leaf material had insufficient leaf area to provide adequate quantities of fixed carbon for grass plant restoration. Because of the deficient availability of carbon, the weight of the leaf biomass removed by defoliation was not replaced by compensatory processes and fewer vegetative tillers were produced than that developed on the ungrazed control treatment (Manske 2010a, 2010b, 2014a, 2014b).

Removal of 25% of the leaf material from grass tillers between the three and a half new leaf stage and the flower stage caused an increase in the quantities of exudates containing simple carbon energy to be released from partially defoliated grass tillers through the roots into the rhizosphere to be great enough to significantly increase the rhizosphere volume in a grazing treatment study (Gorder, Manske, Stroh 2004) and to significantly increase the rhizosphere weight by the third year after initiation of the activation treatment in a prairie restoration study (Manske 2013).

Removal of 25% of the leaf material by partial defoliation of grass tillers between the three and a half new leaf stage and the flower stage fully activated the compensatory physiological processes and fully activated the asexual processes of vegetative tiller production when 100 lbs/ac or greater of mineral nitrogen was available. The weight of the leaf biomass removed by partial defoliation was replaced with new leaf growth at a rate of 140% of the lost weight. The quantity of vegetative tiller production increased at a rate of 214% greater tiller density/m² (Manske 2010a, 2010b, 2014a, 2014b). The remaining 75% leaf material of rejuvenated older leaves had sufficient leaf area to fix carbon at adequate quantities for compensatory growth and development of the replacement leaves and shoots. Removal of 25% of the leaf weight during vegetative growth stages also removed sufficient quantities of the growth-inhibiting hormone, auxin, permitting synthesis or utilization of the growth hormone, cytokinin, in the axillary buds and activated growth and development of vegetative tillers from a high percentage of the axillary buds (Manske 2011b).

Activation of the defoliation resistance mechanisms; the compensatory physiological processes and coprocesses, and the asexual processes of vegetative tillering and coprocesses; requires grazing management strategies that specifically include annual activation with partial defoliation by large grazing graminivores that removes 25% to 33% of the aboveground leaf and shoot weight from grass tillers in vegetative phenological growth between the three and a half new leaf stage and the flower stage after 100 lbs/ac of available mineral nitrogen has been mineralized annually by the rhizosphere microorganism biomass that has been enhanced over two or three growing seasons by increased exudate release containing short chain carbon energy from vegetative grass tillers by partial defoliation and after fixed carbon is available in large enough quantities from the leaf area of rejuvenated tillers equal to 75% to 67% of the ungrazed vegetative tiller leaf area.

Summary

Many of the problems found on rangeland pastures are the result of deficiencies in the amount of available mineral nitrogen in the soil. Nongrazing and traditional grazing practices are the origins of these management caused problems.

Rangeland soils are actually not deficient in nitrogen; they contain large quantities of organic nitrogen, but it is not available to higher plants. Nitrogen cycles within rangeland soils from the organic form to the mineral form and back to the organic form through biogeochemical processes: immobilization and mineralization. Immobilization of mineral nitrogen to organic nitrogen requires new growth of plants and microorganisms. Mineralization of organic nitrogen into mineral nitrogen requires soil microorganism decomposition.

These biogeochemical processes are integral to the complex mechanisms developed by grass plants that permit grass tillers to withstand and recover from partial defoliation by large graminivores. These mechanisms are the defoliation resistance mechanisms. The grass plants require large quantities of mineral nitrogen and fixed carbon to be available for the rapid production of new leaves and shoots and the development of vegetative tillers that replace the plant biomass lost by grazing.

Starting the functionality of the defoliation resistance mechanisms is not instantaneous. Adequate quantities of mineral nitrogen and fixed carbon must be available before the mechanisms will start to function. Mineral nitrogen needs to be available at the threshold quantity of 100 lbs/ac or greater. Available mineral nitrogen at these high rates requires a great rhizosphere microorganism biomass that can be maintained through exudation of large quantities of short chain carbon energy from grass tillers that have had partial defoliation by large grazing graminivores while the tillers were at vegetative growth stages between the three and a half new leaf stage and the flower stage. Adequate quantities of available fixed carbon can be provided by the partially defoliated tillers when the combined leaf area of the remaining and rejuvenated leaves is 75% to 67% of the leaf area of ungrazed tillers at vegetative growth stages. This means that the quantity of leaf removal during the defoliation resistance mechanism activation treatment of partial defoliation by large grazing graminivores needs to be 25% to 33% of the vegetative tillers leaf weight. Rangelands with long-term management by traditional grazing practices with moderate stocking

rates typically require two to three growing seasons to increase the rhizosphere microorganism biomass to levels that are capable of mineralizing available mineral nitrogen at rates of 100 lbs/ac. The defoliation resistance mechanisms can then be maintained at full functional levels through grazing management strategies that specifically include annual activation treatments of partial defoliation by large grazing graminivores that remove 25% to 33% of the aboveground leaf weight of grass tillers at phenological growth stages between the three and a half new leaf stage and the flower stage.

Stopping the functionality of the defoliation resistance mechanisms is also not instantaneous. When or if the annual activation treatments are terminated, the functional levels of the defoliation resistance mechanisms fade rapidly to ineffectiveness during the following two or three growing seasons.

Acknowledgment

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

Table 1. Mineral nitrogen (lbs/ac) available on mixed grass prairie ecosystems effected by traditional management treatments.

Traditional Management Treatment	Operational Duration Years	Available Mineral Nitrogen lbs/ac
4.5 m Seasonlong	20 yr	76.7
6.0 m Seasonlong	20 yr	61.6
Deferred Grazing	50 yr	31.2
7.0 m Seasonlong	75 yr	42.4
Nongrazed	75 yr	39.5

Data from Manske 2012a.

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 *Acrobelloides sp.* and *Mesodiplogaster lheritieri* on substrate utilization and nitrogen and phosphorus mineralization. Ecology 62:549-555.
- Anissimov, M. 2013.** What is the evolutionary history of insects?
<http://www.wisegeek.com>.
- Anonymous. 2013.** Grasshopper. Wikimedia Foundation, Inc.
<http://www.en.wikipedia.org>.
- 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.
- 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.
- Bluemle, J.P. 2000.** The face of North Dakota. 3rd edition. North Dakota Geological Survey. Ed. Series 26. 206p. 1pl.
- Box, J.E., and L.C. Hammond. 1990.** Rhizosphere dynamics. Westview Press, Boulder, CO.
- Brady, N.C. 1974.** The nature and properties of soils. MacMillan Publishing Co., Inc., New York, NY. 639p.
- 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. Pflieger. 2002.** Arbuscular mycorrhizal fungi respond to increasing plant diversity. Canadian Journal of Botany 80:120-130.
- Campbell, J.B. 1952.** Farming range pastures. Journal of Range Management 5:252-258.
- 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.
- Chintauan-Marquier, I.C., S. Jordan, P. Berthier, and C. Amedegnata. 2011.** Evolutionary history and taxonomy of a shorthorned grasshopper subfamily: The Melanoplinae (Orthoptera: Acrididae). Molecular Phylogenetics and Evolution 58:22-32.
- 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.
- 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. 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.
- Gomez, R.A., D.C. Lightfoot, and K.B. Miller. 2012.** A phylogenetic review of the North American bandwinged grasshopper genus, *Encoptolophus* Scudder with description of *Nebulatettix* gen. n. (Orthoptera: Acrididae: Oedipodinae). *Insect Systematics and Evolution* 43:117-145.
- 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.
- Headly, H.F. 1975.** Rangeland management. McGraw-Hill Book Company, New York, NY.
- Ingham, R.E., J.A. Trofymow, E.R. Ingham, and D.C. Coleman. 1985.** Interactions of bacteria, fungi, and the nematode 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. 1999.** Grass-tree interactions in western Canada. Ph.D. Dissertation. University of Regina. Regina, Saskatchewan, Canada.
- Kochy, M., and S.D. Wilson. 2000.** Competitive effects of shrubs and grasses in prairie. *Oikos* 91:385-395.
- Langer, R.H.M. 1972.** How grasses grow. Edward Arnold, London, Great Britain.

- 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.
- Li, X., and S.D. Wilson. 1998.** Facilitation among woody plants establishing in an old field. *Ecology* 79:2694-2705.
- 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. 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. 2000a.** Grass growth in height. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 00-3020. Dickinson, ND. 4p.
- 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. 2005.** Evaluation of alfalfa interseeding techniques. NDSU Dickinson Research Extension Center. Rangeland Research Extension Program 4008. 140p.
- Manske, L.L. 2008.** Prehistorical conditions of rangelands in the Northern Plains. NDSU Dickinson Research Extension Center. Summary Range Management Report DREC 08-3015b. Dickinson, ND. 5p.
- 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.** 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. 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., 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. 83p. and Appendix.
- Manske, L.L. 2013.** Initial restoration changes of degraded rangeland with the twice-over rotation grazing strategy. NDSU Dickinson Research Extension Center. Range Research Report DREC 13-1080. Dickinson, ND. 24p.
- Manske, L.L. 2014a.** Grass vegetative tillering responses to partial defoliation. NDSU Dickinson Research Extension Center. Range Research Report DREC 14-1086. Dickinson, ND. 35p.

- Manske, L.L. 2014b.** Vegetative forage tiller development in response to partial defoliation. NDSU Dickinson Research Extension Center. Range Research Report DREC 14-1087. Dickinson, ND. 26p.
- Manske, L.L., and S.A. Schneider. 2014c.** Evaluation of nitrogen fertilization on native rangeland. 2nd Edition. NDSU Dickinson Research Extension Center. Rangeland Research Outreach Program DREC 14-4013b. Dickinson, ND. 193p.
- 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.
- 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.
- 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.
- Peltzer, D.A., and M. Kochy. 2001.** Competitive effects of grasses and woody plants in mixed grass prairie. *Journal of Ecology* 89:519-527.
- 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., and J. Alessi. 1971.** Nitrogen fertilization of semiarid grasslands: plant growth and soil mineral N levels. *Agronomy Journal* 63:277-280.
- Power, J.F. 1972.** Fate of fertilizer nitrogen applied to a Northern Great Plains rangeland ecosystem. *Journal of Range Management* 25:367-371.
- 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.
- 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.
- 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.

- 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. 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.