

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

Llewellyn L. Manske PhD
Range Scientist
North Dakota State University
Dickinson Research Extension Center

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 inorganic (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.

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 early 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 saprophytic 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 (CO₂) 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. 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 (NH₄). The primary symbiotic function of the endomycorrhizal fungi is to nitrify the ammonium (NH₄) excreted by rhizosphere organisms and convert it into nitrate (NO₃), which is an inorganic form of 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 inorganic nitrogen (Coleman et al. 1983, Klein et al. 1988,

Burrows and Pflieger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005).

Inorganic nitrogen is absorbed by plant roots from the surrounding rhizosphere and, through complex processes, the plant combines the inorganic 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 inorganic 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, 2003b). 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 inorganic 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 soluble, 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).

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 inorganic (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 (inorganic) 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 inorganic nitrogen, ammonia (NH₃), ammonium (NH₄), and nitrate (NO₃), with steam distillation (Keeney and Nelson 1982). These quantified values of inorganic nitrogen were converted from parts per million to pounds per acre-foot. Soil nitrite (NO₂) 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 inorganic 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 inorganic 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 inorganic 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 inorganic nitrogen available on the no burns treatment and every-other-year prescribed burning treatments was less than 30% of the inorganic 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 inorganic 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 seasonlong grazing treatment and on the nongrazed control treatment were not significantly different ($P < 0.05$) (table 1, figure 1). After six grazing seasons, the seasonlong grazing treatment did not beneficially affect the rhizosphere organisms and the biogeochemical nitrogen cycle processes and did not increase the quantity of available inorganic nitrogen. The mineral nitrogen available on the twice-over rotation treatment was high and was significantly greater ($P < 0.05$) than that on the 4.5-m seasonlong grazing treatment and on the nongrazed control treatment (table 1, figure 1). The twice-over rotation treatment beneficially affected the rhizosphere organisms and the available inorganic nitrogen was increased 67.7% greater than on the nongrazed treatment and 59.1% greater than on the seasonlong grazing treatment.

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 inorganic nitrogen 87.7%, 54.6%, and 60.8% greater than that on the nongrazed treatment, respectively.

Rhizosphere volume in cubic feet per acre-foot ($\text{ft}^3/\text{ac-ft}$) 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 inorganic 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 flowering 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 inorganic 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

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); 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) that help grass tillers withstand and recover from partial defoliation by grazing. Foliage removal disrupts plant growth and photosynthesis. Compensatory physiological processes are triggered by seasonable defoliation of grass tillers during phenological growth between the three and a half new leaf stage and the flowering (anthesis) stage activating; 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); 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 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). The phenological growth stage and the degree of foliage removal determines whether the grass tiller responds positively or negatively to defoliation. 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 tillers and grassland ecosystem.

Preseasonable defoliation (April and May) is antagonistic to grass tiller growth and development and to rhizosphere organism activity. 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. The remaining photosynthetically active leaf area 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 or burned 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).

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 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. Almost all of the carbon and some of the nitrogen used for replacement leaf growth and physiological recovery from defoliation are allocated not from material stored in the roots but from remaining shoot tissue and current photosynthetic product (Ryle and Powell 1975, Richards and Caldwell 1985, Briske and Richards 1995, Coyne et al. 1995).

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.

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 flowering (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 and a low proportion of structural carbohydrates (Manske 1996). A greater quantity of inorganic 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 Pflieger 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 inorganic nitrogen is available from the media around the root. Inorganic nitrogen absorption by the roots greatly increases for several days following partial defoliation of grass tillers (Manske 1999a).

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).

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).

Burning or 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. When the standing herbage on a grassland is burned or 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).

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 inorganic 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 inorganic nitrogen after 35

years of treatment. The 6.0-m seasonlong grazing strategy caused a 51.2% decrease in rhizosphere volume after 20 years of seasonlong treatment. The 4.5-m seasonlong grazing strategy did not cause a decrease in inorganic nitrogen after 6 years of treatment but 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 inorganic 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 inorganic nitrogen.

The quantity of inorganic nitrogen on the prescribed burning treatments and no burns treatment was not different, and was less than 30% of the quantity of inorganic 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 inorganic 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 inorganic 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.

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 older 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 established grass basal cover, from the insignificant contribution by true seedlings to the replacement of lost 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.

Full growing season rest and multiple season nongrazing are management choices that withhold defoliation from grasslands. 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 brome grass 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. Removal of grazing from grasslands for one season or for several seasons causes reductions of root biomass and accumulations of standing dead leaf material resulting in decreased plant density and herbage production.

The nongrazed treatment was used as the standard for evaluation of the effects from grazing and burning treatments on rhizosphere organism activity and available inorganic nitrogen. Nevertheless, removal of grazing from grasslands is not beneficial and causes accumulations of dead leaves and reductions of live root biomass, live aboveground 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. 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).

Degraded grassland ecosystems have an increasing composition of opportunistic introduced grasses, early succession and weedy forbs, and shrubs. 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 western snowberry 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 inorganic nitrogen. Reduction of grass plant health and competitiveness follows behind this degradation of biogeochemical processes and the reduction of available inorganic 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 "weedy" plant species (Manske 2007c). 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).

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 inorganic nitrogen was not increased by any of the prescribed 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 inorganic 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 inorganic 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 inorganic 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 inorganic 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 inorganic 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 flowering (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 inorganic nitrogen. 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 inorganic 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.

Acknowledgment

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

Table 1. Mineral nitrogen (lbs/acre-foot) for grazing treatments and repeated every-other-year burning treatments and rhizosphere volume (ft³/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) | | 49.75 z |
| 4.5-m Seasonlong (4.5-m SL) | 111.76 b | 67.61 yz |
| Twice-over Rotation (TOR) | 177.84 a | 227.06 x |
| Burning Treatments | | |
| No Burns | 31.20 c | |
| One Burn | 31.49 c | |
| Two Burns | 30.71 c | |
| Three Burns | 18.08 c | |
| Four Burns | 27.28 c | |
| Early Spring Burns | 11.88 | |
| Spring Burns | 27.64 c | |
| Early Summer Burns | 30.74 c | |
| Mid Summer Burns | 23.14 c | |

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 ($P < 0.05$).

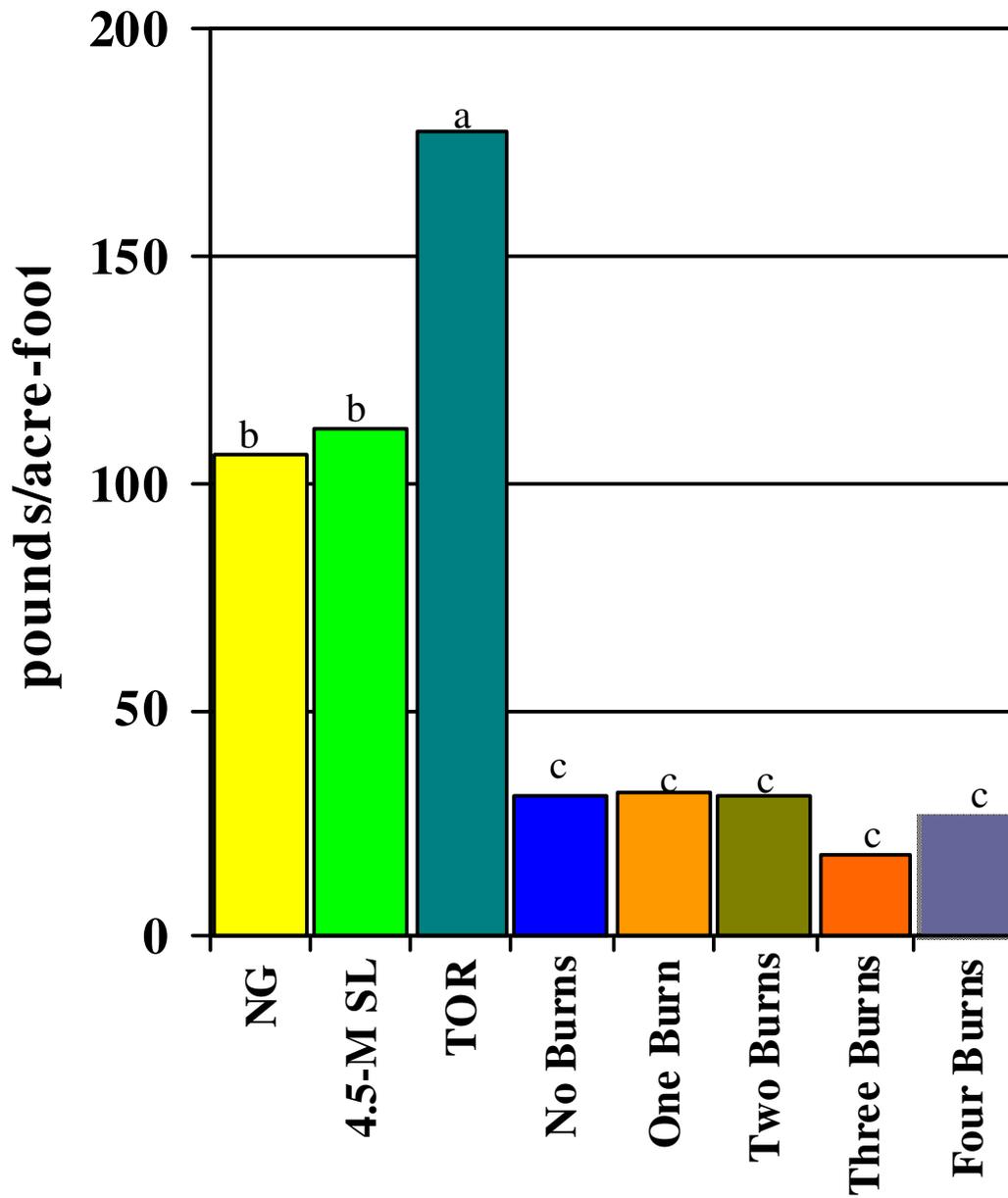


Figure 1. Mineral nitrogen in pounds per acre-foot for grazing treatments and every-other-year burn treatments.

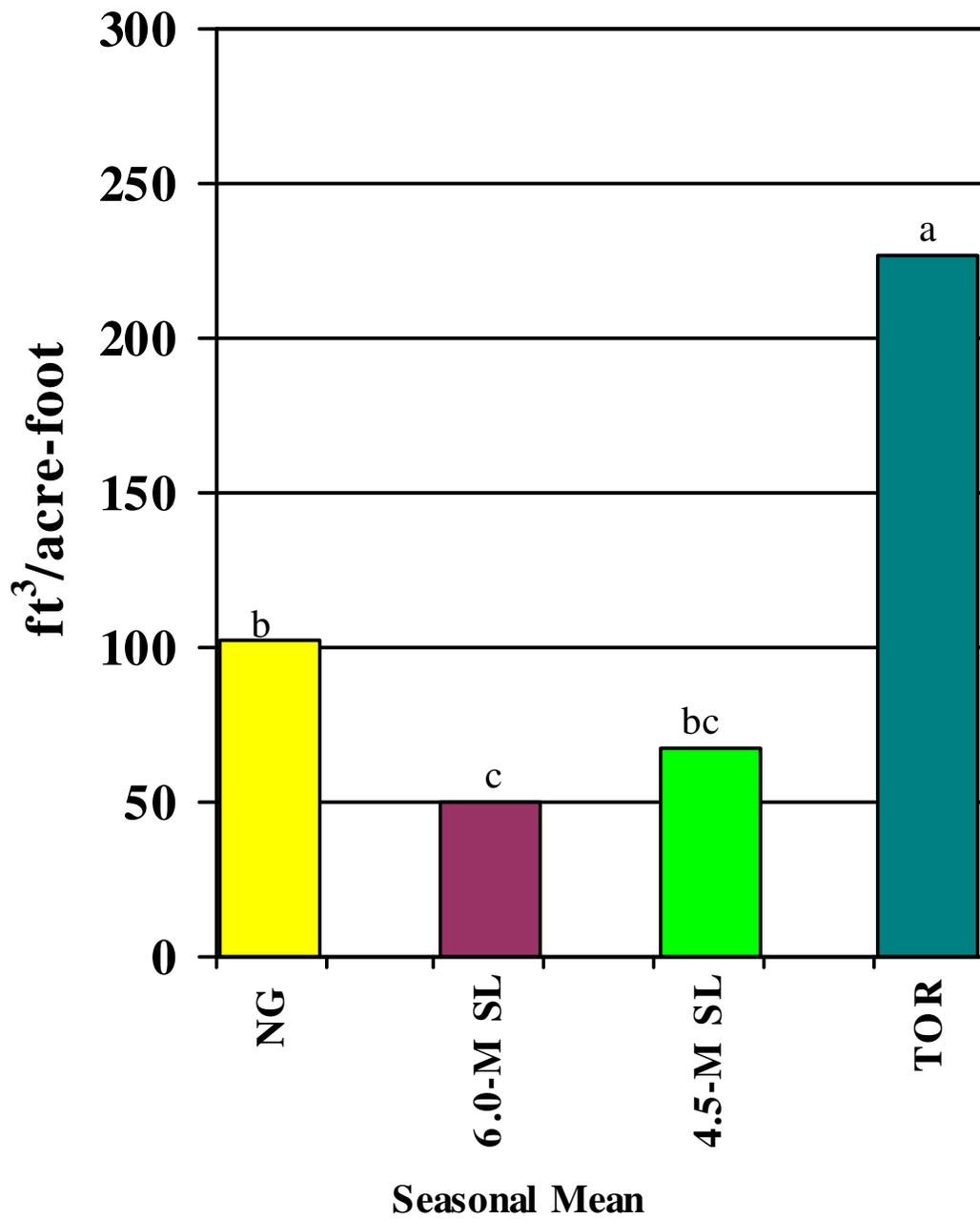


Figure 2. Seasonal mean rhizosphere volume in cubic feet per acre-foot for grazing treatments.

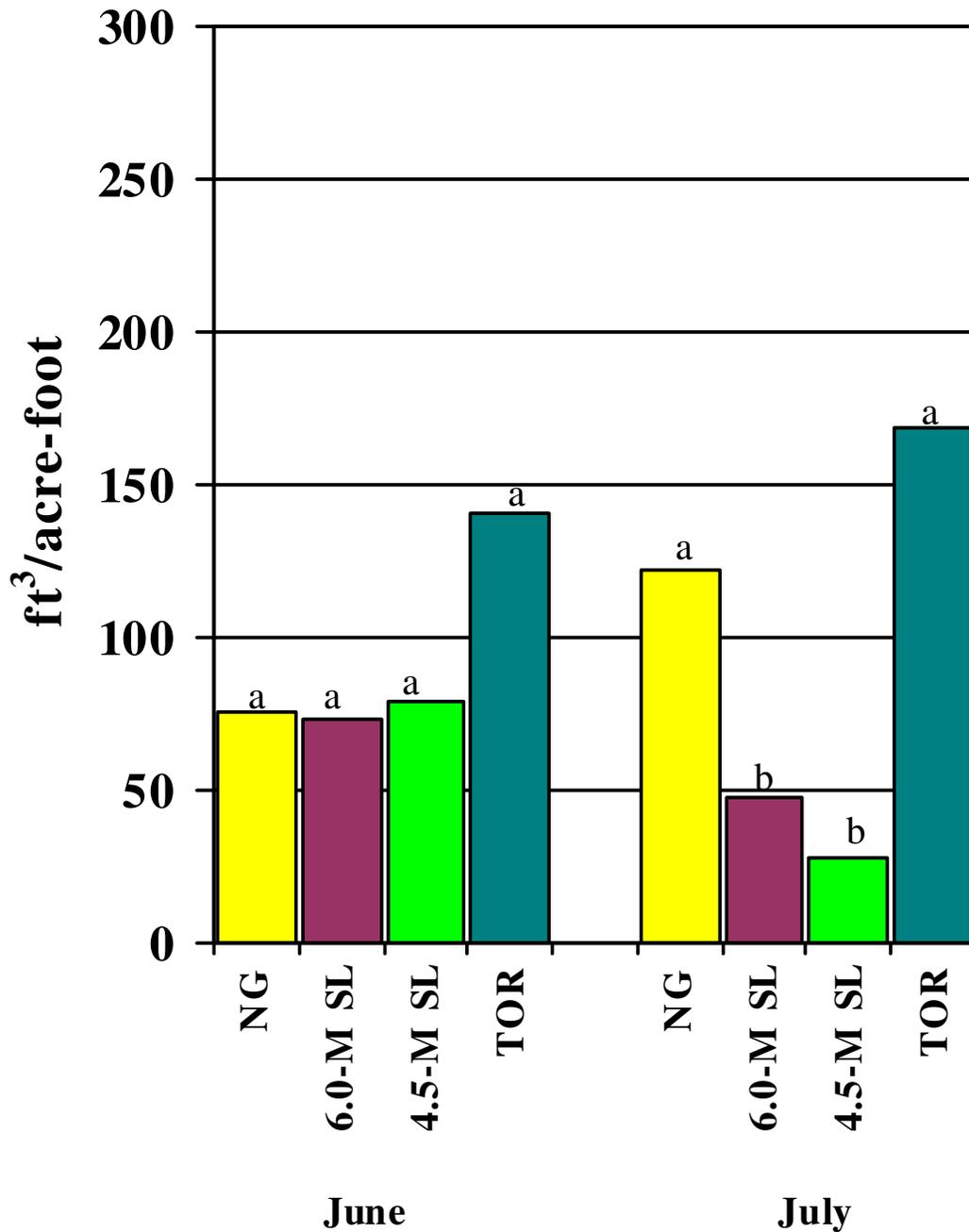


Figure 3. Monthly rhizosphere volume in cubic feet per acre-foot during June and July for grazing treatments.

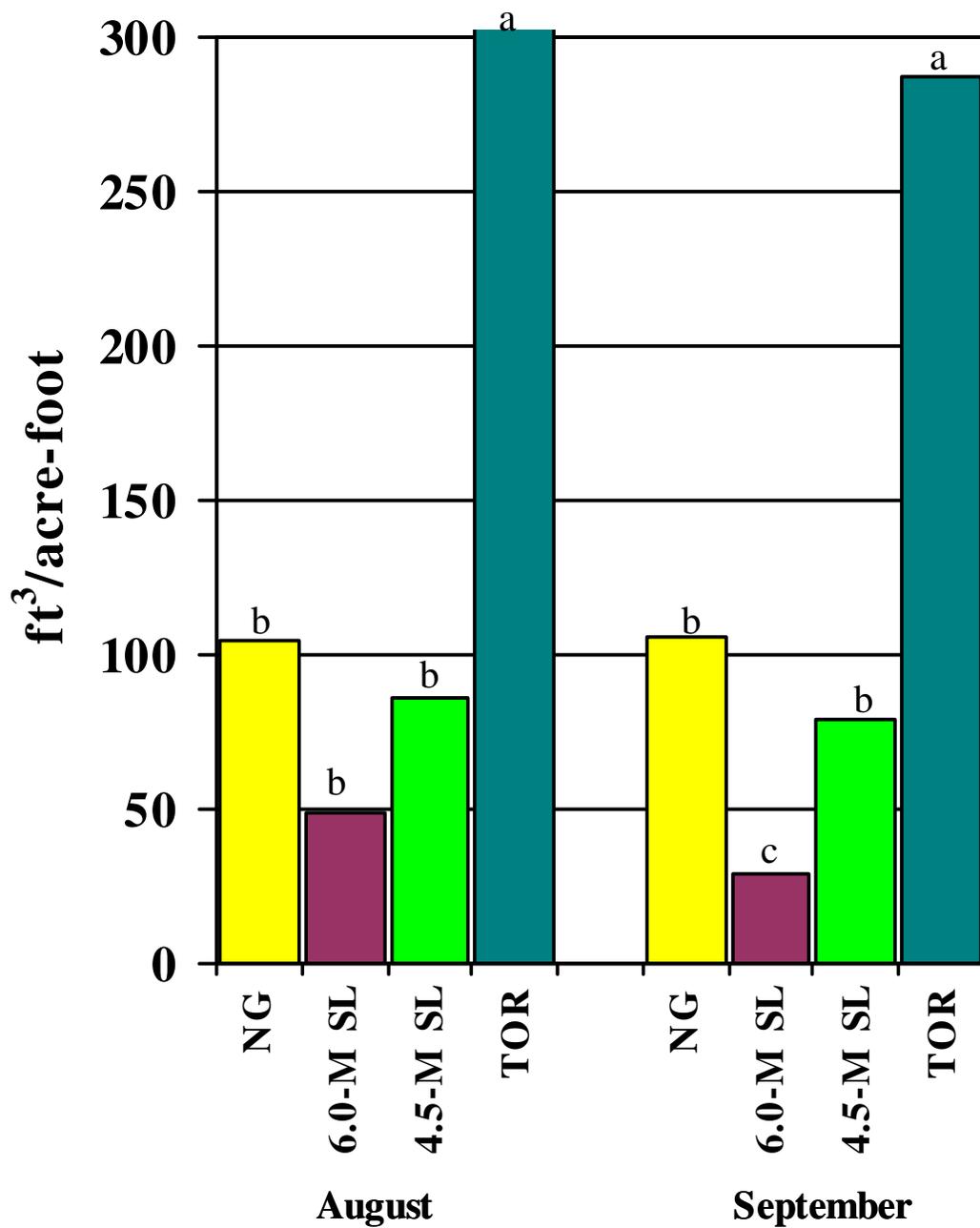


Figure 4. Monthly rhizosphere volume in cubic feet per acre-foot during August and September for grazing treatments.

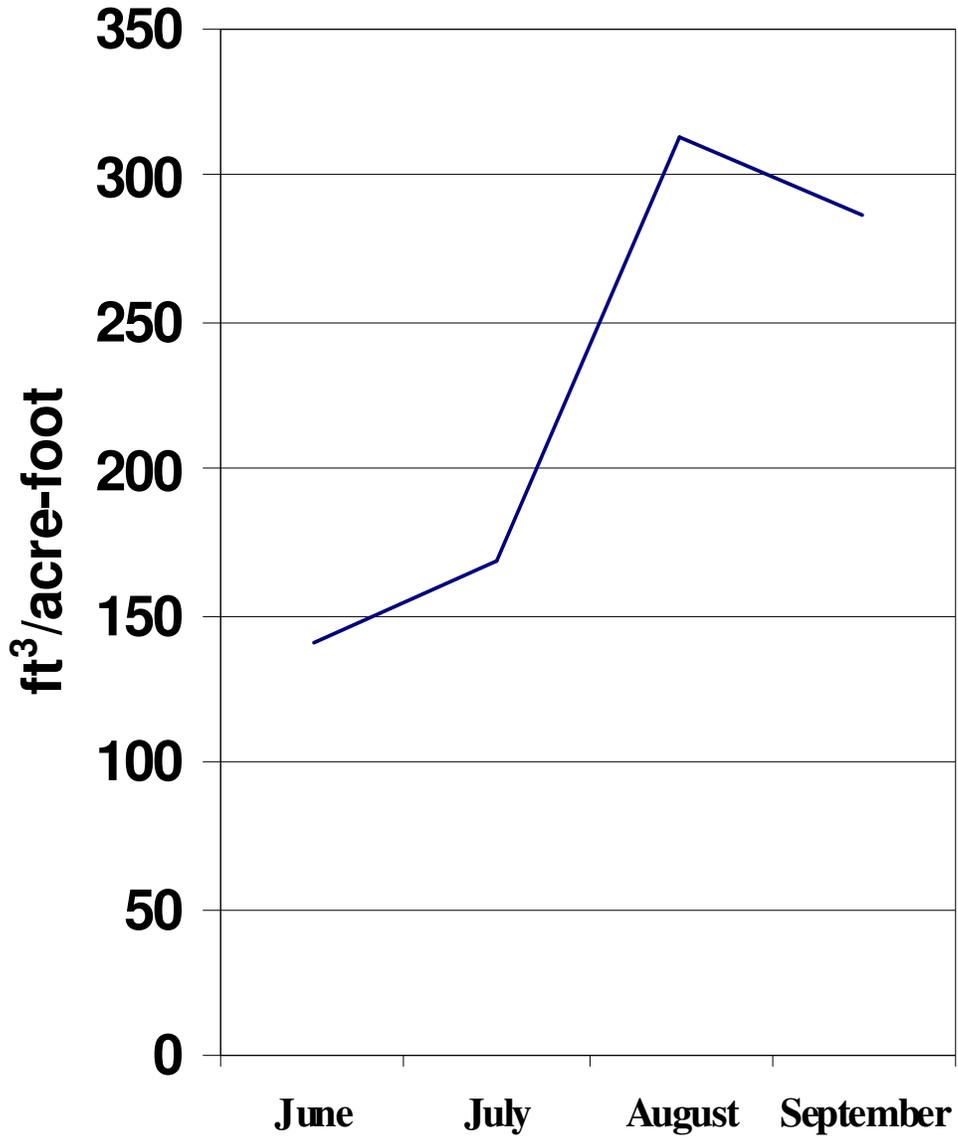


Figure 5. Rhizosphere volume change on the twice-over rotation treatment third pasture that was grazed for 15 days during early July.

Literature Cited

- 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.
- Barker, W.T., and W.C. Whitman. 1988.** Vegetation of the Northern Great Plains. *Rangelands* 10:266-272.
- 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.
- 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.
- 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, 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.
- 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.
- 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.
- 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.
- 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.
- 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. 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. 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 grazing management treatments on rangeland vegetation. NDSU Dickinson Research Extension Center. Summary Range Research Report DREC 03-3027. Dickinson, ND. 6p.
- 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.

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