Biology of Defoliation by Grazing

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

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

Grass Tiller Development

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

Phytomers develop from leaf primordia that form on alternating sides of the apical meristem (Evans and Grover 1940, Langer 1972, Beard 1973, Dahl 1995). Almost all of the phytomer cells are produced in the apical meristem while the leaf primordia is a minute bud (Langer 1972). The oldest cells of a leaf are at the tip, and the youngest cells are at the base (Langer 1972, Dahl 1995). Several leaf primordia are at various stages of development at any one time. The oldest leaf is outermost, while younger leaves grow up through existing leaf sheaths (Rechenthin 1956, Beard 1973). Growth of the leaf results through cell enlargement and elongation (Esau 1960, Dahl 1995). A few new cells are produced by intercalary meristem located at the base of the blade, the base of the sheath, and the base of the internode (Esau 1960). Cell expansion occurs in the region protected by the sheaths of older leaves. When the cells emerge and are exposed to light, expansion ceases and photosynthesis and transpiration begin (Langer 1972). Once a leaf blade is fully expanded, no further growth of that blade is possible (Dahl 1995).

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

Longevity of grass tillers generally does not exceed two growing seasons (Langer 1956, Butler and Briske 1988). Production of new leaf primordia

continues until the status of the apical meristem changes from vegetative to reproductive. Sexual reproductive growth can begin after the tiller has attained a certain minimum amount of vegetative development (Dahl 1995). Initiation of the reproductive growth stage is triggered by photoperiod (Roberts 1939, Leopold and Kriedemann 1975, Dahl 1995) but can be slightly modified by temperature and precipitation (McMillan 1957, Leopold and Kriedemann 1975, Dahl and Hyder 1977). Most tillers initiate vegetative growth during the previous growing season, overwinter, resume growth the subsequent growing season, become florally induced, and proceed with development of sexual reproductive structures (Briske and Richards 1995). When the florally induced grass tiller is between the third new leaf stage and three and a half new leaf stage, the apical meristem ceases to produce leaf primordia and begins to produce flower primordia (Frank 1996, Frank et al. 1997). Previously formed leaf buds continue to grow and develop (Esau 1960, Langer 1972). Many domesticated cool-season grasses reach the three and a half new leaf stage around late April to early or mid May. Most native cool-season grasses reach the three and a half new leaf stage around early June, and most native warm-season grasses reach the three and a half new leaf stage around mid June (Manske 1999a).

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

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

Procurement of Elemental Resources

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

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

The source of carbon for plant growth is atmospheric carbon dioxide (CO_2). Plants capture and fix carbon with the hydrogen from soil water during the process of photosynthesis which converts

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

The source of nitrogen for plant growth is mineral nitrogen (NO_3, NH_4) converted from soil organic nitrogen by rhizosphere organisms. Low quantities of available mineral nitrogen limits productivity more often than water on grassland ecosystems (Tilman 1990). Increasing rhizosphere organism activity increases the quantity of available mineral nitrogen. Mineral nitrogen is absorbed by plant roots. The grass plant uses mineral nitrogen to produce proteins. Plant crude protein can be used by herbivores that consume grass plant parts. Organic nitrogenous compounds comprising herbivore excreta or dead plant material are returned to grassland soils. Transforming nitrogen from organic nitrogen to mineral nitrogen and back to organic nitrogen is complex and has a great impact on many organisms at multiple trophic levels and has high biological costs on the ecosystem resources.

Defoliation Resistance Mechanisms

The key factor in meeting grass plant biological requirements is proper timing of defoliation. The effects of defoliation are not simply the removal of herbage from grass plants (Langer 1963, 1972): foliage removal disrupts plant growth and photosynthesis, and defoliation also changes physiological processes in all parts of the plant; alters the plant community microclimate by changing light transmission, moisture relations, and temperature; and changes the soil environment, thereby affecting soil organism activity (Manske 2000a). Grass plants have developed defoliation resistance mechanisms in response to grazing during the period of coevolution with herbivores (McNaughton 1979, 1983; Coleman

et al. 1983; Briske 1991; Briske and Richards 1995; Manske 1999a). The defoliation resistance mechanisms help grass tillers withstand and recover from partial defoliation by grazing. These mechanisms are: herbivore-induced compensatory physiological processes (McNaughton 1979, 1983; Briske 1991); stimulation of vegetative reproduction of secondary tillers from axillary buds (Mueller and Richards 1986, Richards et al. 1988, Murphy and Briske 1992, Briske and Richards 1994, Briske and Richards 1995); and stimulation of rhizosphere organism activity and the increased conversion of mineral nitrogen from soil organic nitrogen (Coleman et al. 1983, Ingham et al. 1985).

Compensatory Physiological Processes

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

Activity of meristematic tissue is enhanced and growth rates of replacement leaves and shoots increases following partial defoliation. The rate of leaf area expansion following defoliation is determined by interactions among meristem type, environmental variables, and resource availability (Briske and Richards 1995). Growth is most rapid from intercalary meristem, intermediate from apical meristem, and slowest from axillary buds (Briske and Richards 1995). Developing leaf primordia not fully expanded at time of defoliation have increased growth rates and tend to grow larger than leaves on undefoliated tillers (Langer 1972). The photosynthetic rate of the replacement leaves is higher than that of same-age foliage on undefoliated tillers (Briske and Richards 1995).

Defoliated tillers increase photosynthetic rates of remaining foliage (Briske and Richards 1995). This compensatory photosynthesis can be induced by changes in light quality and intensity that result from grazing modifications in the microhabitat

and by modifications of physiological functions caused by the indirect effects resulting from increased root-shoot ratio and mediated by cytokinins and other signals produced in the root (Briske and Richards 1995). These changes appear to affect leaf development and aging. The photosynthetic apparatus is rejuvenated, the leaf senescence rate is inhibited or reduced, and the lifespan of leaves is increased (Briske and Richards 1995). Remaining mature leaves on defoliated tillers frequently develop increased leaf mass per unit area shortly after defoliation (Briske and Richards 1995).

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

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

rhizosphere organisms is required for full activation of the compensatory physiological processes in partially defoliated grass tillers (Manske 2009, 2010).

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

Vegetative Reproduction by Tillering

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

Meristematic activity in axillary buds and the subsequent development of vegetative tillers is regulated by auxin, a growth-inhibiting hormone produced in the apical meristem and young developing leaves of lead tillers (Briske and Richards 1995). The physiological process by which the lead

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

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

If no defoliation occurs before the flower (anthesis) stage, the lead tiller continues to hormonally inhibit secondary tiller development from axillary buds. Production of the inhibitory hormone, auxin, declines gradationally as the lead tiller reaches the flower stage. The natural reduction of auxin in the lead tiller usually permits only one secondary tiller to develop from the potential of 5 to 8 buds. This developing secondary tiller produces auxin in the apical meristem and young developing leaves that hormonally suppresses development of additional axillary buds.

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

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

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

Rhizosphere Organism Activity

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

ecosystems, the conversion of plant usable mineral nitrogen from soil organic nitrogen requires active rhizosphere organisms. Rhizosphere organism activity requires short chain carbon exudates from roots of grass plants. Rhizosphere organisms trade nitrogen to grass plants for carbon, and grass plants trade carbon to soil microorganisms for nitrogen. This interdependent symbiotic relationship between grass plants and rhizosphere organisms is controlled by partial defoliation of aboveground plant parts by large grazing herbivores.

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

The activity of rhizosphere organisms increases along the trophic hierarchy, starting with the bacteria. Bacteria are microscopic single-celled saprophitic organisms that consume large quantities of soil organic matter and are one of the primary producers of the rhizosphere. The increased biomass and activity of the bacteria elevates the concentration of carbon dioxide (CO_2) resulting in stimulation of activity in the other rhizosphere organisms. Protozoa are single-celled microorganisms that are mainly small amoeba and feed primarily on bacteria. Nematodes are a diverse group of small nonsegmented worms. Most nematodes feed primarily on bacteria or fungi, some feed on protozoa, and some eat other nematodes. Springtails are the most abundant insect in grassland soils and they travel among rhizosphere structures. Minute springtails ingest considerable quantities of soil

organic matter in order to eat fungi and bacteria. Mites are small eight-legged arachnids that travel among rhizosphere structures and feed on fungi, nematodes, small insects, and other mites. Mites help distribute fungus spores and bacteria through the soil by carrying them on their exoskeleton. Endomycorrhizal fungi are the other primary producers of the rhizosphere and are achlorophyllous saprophytes that live on dead organic matter and can not fix carbon because they lack chlorophyll. The bacteria and fungi are the microflora saprotrophic organisms at the bottom of the food chain and makeup the greatest biomass of the rhizosphere. Both bacteria and fungi contain high proportions of nitrogen in relation to their carbon content. The rhizosphere organisms of the microfauna trophic levels graze on bacteria or fungi and ingest greater quantities of nitrogen than they need for a balanced diet based on energy (carbon); the excess nitrogen is excreted as ammonium (NH_4). The primary symbiotic function of the endomycorrhizal fungi is to nitrify the ammonium (NH_4) excreted by rhizosphere organisms and convert it into nitrate (NO_3), which is a form of mineral nitrogen usable by grass plants. The elevated rhizosphere organism activity caused by the increase in available carbon compounds results in a greater quantity of organic nitrogen converted into mineral nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005).

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

Along with the improvement of ecosystem biogeochemical processes and the resulting increase in available mineral nitrogen, the increase of mycorrhizal fungi biomass and activity benefits other grassland ecosystem functions. Endomycorrhizal fungi develop arbuscules, vesicles, and hyphae within root tissue of the host plant (Harley and Smith 1983) and secrete adhesive polysaccharides that bond soil particles around grass roots forming the structural

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

Effects from Seasonality of Defoliation by Grazing

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

No Defoliation by Grazing

Full growing season rest and multiple season resting are antagonistic management choices that withhold defoliation from grasslands. The term "rest" is a misnomer because the common inference that "resting" a grassland by removal of defoliation causes revitalization of crucial processes is inaccurate. Resting a grassland by withholding defoliation causes regression of ecosystem biogeochemical processes and results in the deterioration of grassland ecosystems. Two negative changes occur relatively soon after grazing management is removed; live root biomass decrease (Whitman 1974, Brand and Goetz 1986) and standing dead leaves accumulate (Brand

and Goetz 1986). The reduction of active root surface area causes a reduction in root length for interaction with rhizosphere organisms and causes a decrease in absorption of water and nutrients from the soil, resulting in a reduction in growth of aboveground plant parts. The accumulating standing dead leaves shade the lower leaves, increasing the rate of leaf senescence and reducing the rate of photosynthesis, causing a decrease in the supply of carbohydrates that results in a reduction in growth of leaves and roots (Langer 1972, Briske and Richards 1995). Grass leaves grown under shaded conditions become longer but narrower, thinner (Langer 1972, Weier et al. 1974) and lower in weight (Langer 1972) than leaves in sunlight. Shaded grass plants shift to erect growth forms with a small number of larger tillers (Briske and Richards 1995). Lack of grazing reduces grass tiller densities by decreasing tiller development and increasing tiller mortality through shading (Grant et al. 1983). After a few years, shading reduces the composition of native grass species in the ecosystem and increases the composition of shade-tolerant or shade-adapted replacement species, like smooth bromegrass and Kentucky bluegrass.

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

Prae Seasonable Defoliation by Grazing

Preseasonable defoliation, before the three and a half new leaf stage (April and May), is antagonistic to grass tiller growth and development and to rhizosphere organism activity. Secondary tillers of cool-season and warm-season grasses with apical meristem status remaining vegetative and fall initiated cool-season grass tillers survive overwinter on carbohydrate reserves that were stored by the tiller during the winter hardening process that occurs between mid August and mid October. Spring growth during the second growing season for these carryover tillers, reclassified as lead tillers, depends both on carbohydrate reserves and on photosynthetic products from the portions of previous years leaves that overwintered without cell wall rupture and regreened with chlorophyll. Spring growth for fall developed tiller buds of warm-season grasses depends initially on carbohydrate reserves and later both on carbohydrate reserves and on photosynthetic product from new young leaves. Grass tiller growth and development depend, in part, on adequate carbohydrate reserves in early spring because the amount of photosynthetic product synthesized by the carryover leaves and the first couple of early growing new leaves is insufficient to meet the requirements for leaf growth (Heady 1975, Coyne et al. 1995). Grass growth also requires that the tiller maintains adequate leaf area with a combination of carryover leaves and new leaves to provide photosynthetic product for growth of sequential new leaves. The total nonstructural carbohydrates of a grass tiller are at low levels following the reduction of reserves during the winter respiration period, and the carbohydrate reserves remaining in the roots and crown are needed for both root growth and initial leaf growth during early spring. The low quantity of reserve carbohydrates may not be adequate to supply the entire amount required to support root growth and also support leaf growth causing a reduction in active growth until sufficient leaf area is produced to provide the photosynthetic assimilates required for plant growth and other processes (Coyne et al. 1995). Removal of aboveground material from grass tillers not yet at the three and a half new leaf stage deprives tillers of foliage needed for photosynthesis and increases the demand upon already low levels of carbohydrate reserves. Delays in spring grass growth are management-induced problems.

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

Early Seasonable Defoliation by Grazing

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

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

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

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

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

Mid and Late Seasonable Defoliation by Grazing

Mid and late seasonable defoliation, after lead tillers have flowered and started to develop seeds (mid July to mid October), is not as beneficial as early seasonable defoliation. Activation by defoliation of the compensatory physiological processes diminishes and removed foliage is not completely replaced. However, mature grass plants can tolerate removal of up to 50% of the aboveground plant material. During middle and late phenological growth stages, the defoliation resistance mechanisms

are still triggered by defoliation by grazing of grass tillers (Manske 1999a), but because the aboveground tiller material consists of a high proportion of structural carbohydrates (fiber) and a low quantity of nitrogen (crude protein) (Manske 1996) and leaf senescence has caused decreased photosynthetic and physiological activity with very little or no carbon exudation into the rhizosphere, the compensatory physiological processes are not fully executed. Moreover, the general decreases in soil water level typical of the middle and late portions of the grazing season limit biological processes and rhizosphere organism activity (Curl and Truelove 1986, Bazin et al. 1990).

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

Vegetative tiller growth is the dominant form of reproduction in semiarid and mesic grasslands (Belsky 1992, Chapman and Peat 1992, Briske and Richards 1995, Chapman 1996, Manske 1999a) not sexual reproduction and the development of seedlings. Recruitment of new grass plants developed from seedlings is negligible in healthy grassland ecosystems. The frequency of true seedlings is extremely low in functioning grasslands, and establishment of seedlings occurs only during years with favorable moisture and temperature conditions (Wilson and Briske 1979, Briske and Richards 1995), in areas of reduced competition from vegetative tillers, and when resources are readily available to the growing seedling. Sarvis (1941) was unable to determine any improved benefit to grass plant density from reseeding of the grasses after 23 years of deferred grazing treatment. Manske et al. (1988), in a three year study, found that total grass basal cover decreased significantly after one year of deferred grazing treatment. Grassland ecosystems are negatively affected by deferred grazing management from the significant yearly decrease of grass basal cover, grass density, and herbage production, and from the loss of significant energy and resources used for the increased inutile seed production that could have been supplied for increased vegetative tiller production.

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

Post Seasonable Defoliation by Grazing

Post seasonable defoliation (mid October to March) is not harmful to senescent lead tillers that have produced seeds. However, the lead tillers that did not produce seeds, the secondary tillers, and the fall initiated tillers that will be the future lead tillers of the next growing season are injured by late season defoliation. Secondary tillers with the apical meristem at vegetative status and fall initiated cool-season grass tillers overwinter and resume active growth as lead tillers during early spring of the subsequent growing season. Winter survival and spring regrowth of secondary tillers and fall tillers depend on having adequate carbohydrate reserves. The quantity of carbohydrates stored during the winter hardening process is closely related to the amount of active leaf material on each tiller. Tillers with abundant leaf area during late summer and early fall can store adequate quantities of carbohydrates to survive the winter and produce robust leaves the following spring. Winter dormancy in perennial

grasses is not total inactivity, but reduced activity (Leopold and Kriedemann 1975). The crown, portions of the root system, and some leaf tissue remain active and maintain physiological processes throughout the winter by using stored carbohydrates. Cool-season grasses continue leaf growth at slow rates during the winter. Severe grazing of grass tillers during August to mid October removes sufficient leaf material from secondary tillers and fall tillers to cause inadequate quantities of carbohydrates to be stored. Plants that have low carbohydrate reserves and survive the dormancy period produce tillers with reduced height and weight.

Some tillers with low carbohydrate reserves do not survive until spring. The rate at which plants respire, or use, stored carbohydrates during the winter is affected by the amount of insulation standing plant material and snow provide from the cold winter air temperatures. The greater the amount of insulation, the more slowly the plant draws on its carbohydrate reserves. When the standing herbage on a grassland is grazed short and most of the snow is blown off, very rapid respiration can occur and deplete carbohydrate reserves before spring, causing tiller death called "winter kill".

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

Degraded Grassland Ecosystem Restoration

The primary cause of degradation of prairie ecosystems and the reduction of grassland productivity is management practices that are antagonistic to the ecosystems' living components of grassland plants and soil organisms and that are detrimental to the compensatory physiological processes, the vegetative reproduction mechanisms,

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

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

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

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

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

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

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

The composition of opportunistic grasses and forbs will decrease as a result of the increasing competition from native grass plants as the available mineral nitrogen increases from the increasing rhizosphere organism biomass and activity and from the increasing vegetative reproduction by tillering the native grass density and herbage biomass production

improves. The restoration of ecosystem biogeochemical processes of nutrient cycling is followed by the improvement in plant species composition and the increase in grassland ecosystem productivity.

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

Implications for Management of Defoliation by Grazing

Productivity on grassland ecosystems depends on the level of rhizosphere organism activity, on the quantity of available mineral nitrogen converted from soil organic nitrogen to be 100 lbs/ac or greater, on the effectiveness of compensatory physiological processes within grass tillers that increase photosynthetic leaf area through increased growth rates, and on the increased secondary tiller production through vegetative reproduction. Management of partial defoliation by grazing that focuses on meeting the biological requirements of the grass plants and of the rhizosphere organisms is beneficial, and enhances the health and productivity of grassland ecosystems.
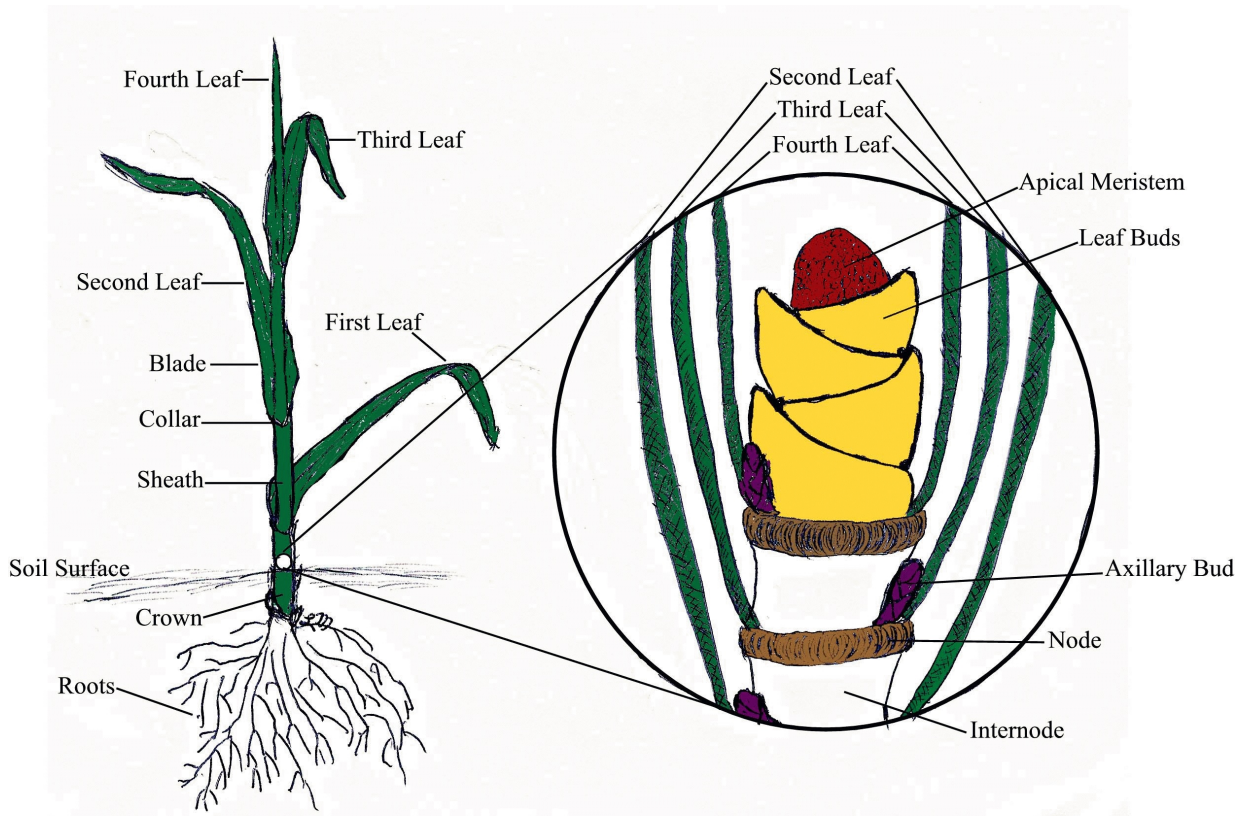
Biologically effective grazing management activates the defoliation resistance mechanisms. Partial defoliation controlled with the twice-over rotation grazing management strategy that removes 25% to 33% of the leaf material from grass tillers at phenological growth between the three and a half new leaf stage and the flower (anthesis) stage (early June to mid July); stimulates compensatory physiological processes resulting in greater replacement leaf, shoot, and root growth; stimulates vegetative reproduction by tillering resulting in greater grass tiller density and herbage biomass production; and stimulates rhizosphere organism biomass and activity resulting in greater quantities of available mineral nitrogen. The twice-over rotation grazing management system uses three to six native rangeland pastures. Each of the pastures in the rotation is partially defoliated by grazing for 7 to 17 days during the first period, the 45-day interval from 1 June to 15 July when grasses are between the three and a half new leaf stage and

flower (anthesis) stage. The length in number of days of the first grazing period on each pasture is the same percentage of 45 days as the percentage of the total season's grazable forage each pasture contributes to the complete system. During the second grazing period when lead tillers are maturing and defoliation by grazing is only moderately beneficial, after mid July and before mid October, each pasture is grazed for double the number of days it was grazed during the first period. Livestock are removed from the native rangeland pastures in mid October.

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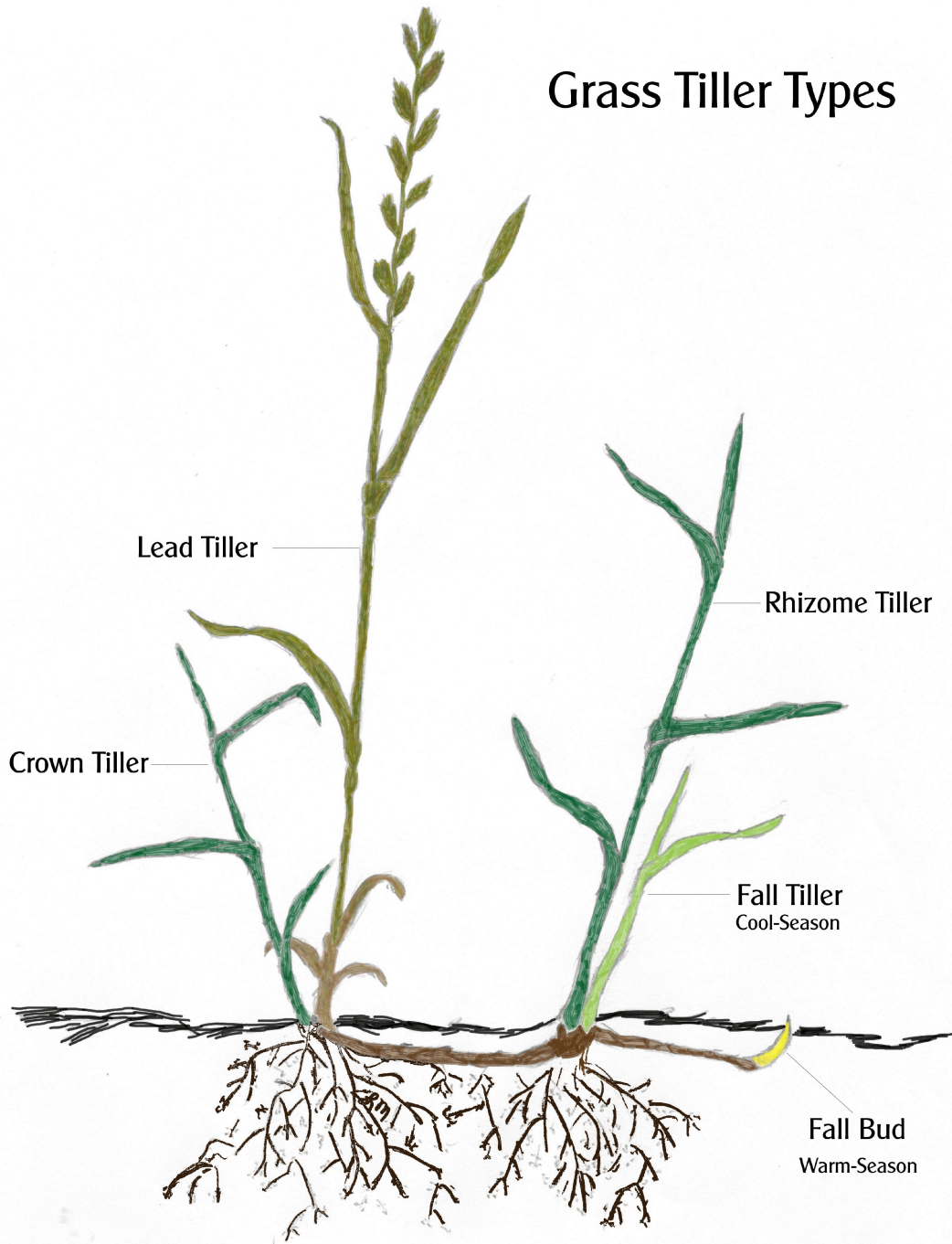
Fourth Leaf

Third Leaf

Second Leaf

First Leaf

Blade

Collar

Sheath

Soil Surface

Crown

Roots

Second Leaf

Third Leaf

Fourth Leaf

Apical Meristem

Leaf Buds

Axillary Bud

Node

Internode

Grass Tiller at 3.5 Leaf Stage

Grass Tiller Types

Lead Tiller

Rhizome Tiller

Crown Tiller

Fall Tiller
Cool-Season

Fall Bud
Warm-Season

SYMBIOTIC RHIZOSPHERE ORGANISMS

RHIZOSPHERE STRUCTURE
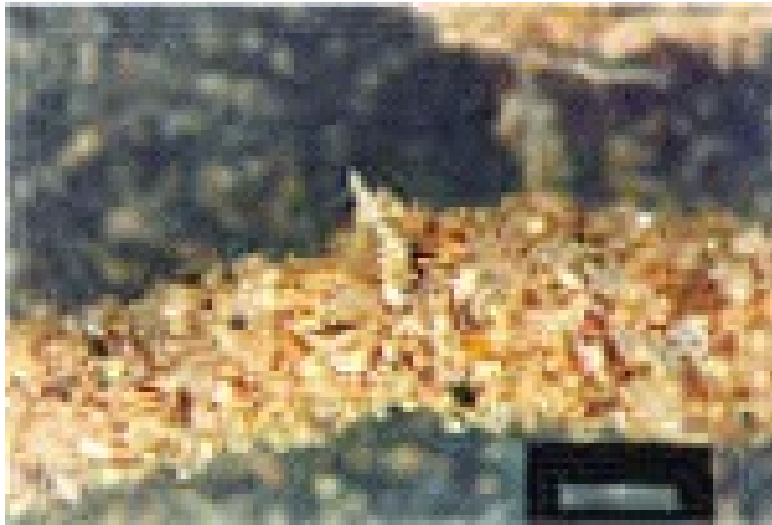
Photo from J. Barrows

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

MICROFLORA
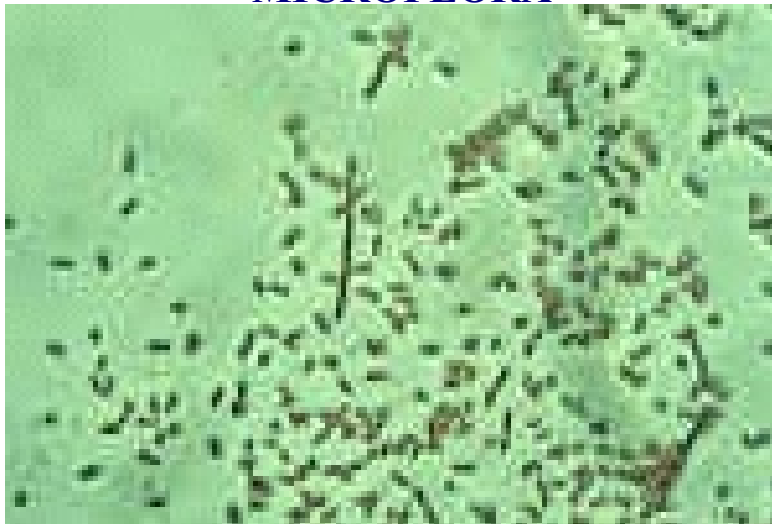
Photo from M.T. Holmes

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

MYCORRHIZAL FUNGI

ENDOMYCORRHIZAL FUNGI

Photo from R. Campbell

Fungal hyphae strands with bacteria on the surface.

Photo from M. Brundrett

Arbuscules and vesicles of a mycorrhizal fungus within root tissue.
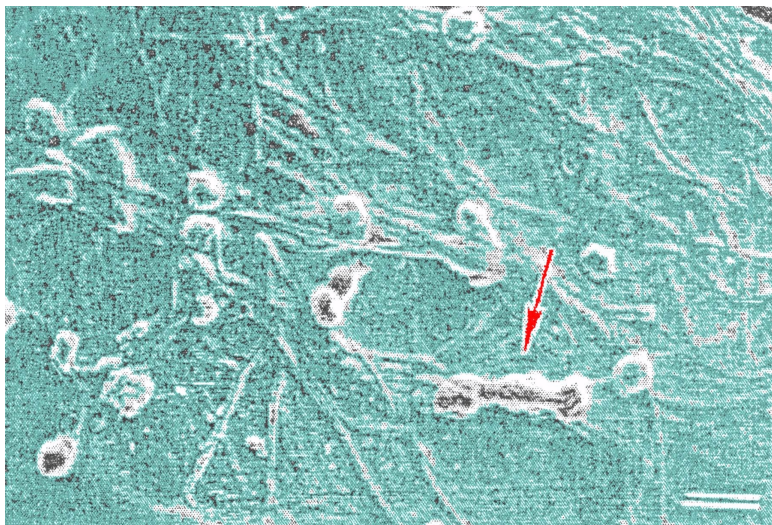
ECTOMYCORRHIZAL FUNGI

Photo from T.C. Caesar-TonThat

Ectomycorrhizal fungus with extracellular polysaccharides.

MICROFAUNA

PROTOZOA

Photo from J.P. Martin

Amoeba ingesting bacteria.
Protozoa are single-celled microorganisms.

NEMATODES

Photo from H. Garrett

Beneficial nematodes are small nonsegmented worms.

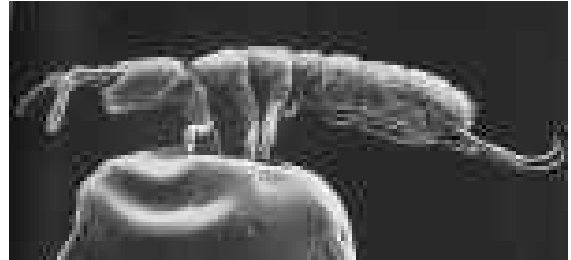# MICROARTHROPODS

SPRINGTAILS

Blind fungal-feeding springtail.

Springtail with furcula released.

Springtails are minute insects.

MITES

Predatory mite.
Mites are small eight-legged arachnids.

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