Rangelands are complex ecosystems consisting of numerous biotic (living) and abiotic (nonliving) components. The biotic components are the grass plants, soil organisms, and grazing graminivores that have biological and physiological requirements. The abiotic components include radiant energy from sunlight and the essential major elements of carbon, hydrogen, nitrogen, and oxygen with separate but closely linked biogeochemical cycles that transform the elements between organic forms and inorganic forms, and with numerous biological, chemical, and atmospheric pathways that transfer the major essential elements into and out of the ecosystem. The minor essential elements consist of seven macrominerals and ten microminerals that are required by most living organisms. The minor elements have biogeochemical cycles or parts of cycles that transform the elements between organic and inorganic forms while they are within an ecosystem. There are numerous pathways that transfer minor essential elements out of an ecosystem. However, there are no readily available natural pathways that can transfer minor essential elements into an ecosystem. After a macromineral or a micromineral has been depleted from a rangeland ecosystem, that soil is deficient of that minor essential element. Rangeland ecosystems are functioning units of coacting biotic organisms interacting with the abiotic components and the environmental factors.

Grass plants, soil organisms, and graminivores have developed complex symbiotic relationships. The grazing graminivores depend on grass plants for nutritious forage. Grass plants depend on rhizosphere organisms for mineralization of essential elements, primarily nitrogen, from the soil organic matter. The main sources of soil organic matter are grazing animal waste and dead plant material. Rhizosphere organisms depend on grass plants for energy in the form of short carbon chains. Grass plants exudate short carbon chain energy through the roots into the rhizosphere following partial defoliation of the aboveground leaf material by grazing graminivores. Grass plants produce double the leaf biomass than is needed by the plant to provide nutritious leaf forage to the grazing graminivores.

Grass Tiller Growth

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

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

Individual leaves of grass tillers are relatively short lived. Young middle-aged leaves are in their prime when the rate of apparent photosynthesis is maximum and the leaves begin exporting assimilates to other parts (Langer 1972). At this point, the leaf has its greatest dry weight. Leaf senescence, or aging, begins shortly after middle age. Senescence begins at the tip, the oldest part of the leaf, and spreads downward. As senescence progresses, apparent photosynthesis and movement of assimilates from the leaf to the other parts of the plant decrease (Langer 1972). The rate of senescence occurs at about the same rate as leaf

appearance but is influenced by environmental conditions. During senescence, cell constituents are mobilized and redistributed to other parts of the plant (Beard 1973). This process causes weight of the leaf to decrease (Leopold and Kriedemann 1975). The percentage of dryness in a leaf blade is an indication of the degree of senescence.

Longevity of grass tillers usually extend two growing seasons (Langer 1956, Butler and Briske 1988, Manske 2009a). Production of new leaf primordia continues until the status of the apical meristem changes from vegetative to reproductive. Sexual reproductive growth begins during the second growing season after the lead tiller has attained a certain minimum amount of vegetative development (Dahl 1995). Initiation of the reproductive growth stage is triggered by photoperiod (Roberts 1939, Leopold and Kriedemann 1975, Dahl 1995) but can be slightly modified by temperature and precipitation (McMillan 1957, Leopold and Kriedemann 1975, Dahl and Hyder 1977). Most secondary vegetative tillers initiate growth during the first growing season, overwinter, resume growth during the second subsequent growing season, become florally induced, and proceed with development of sexual reproductive structures (Briske and Richards 1995). When the florally induced grass lead tiller is between the third new leaf stage and three and a half new leaf stage, the apical meristem ceases to produce leaf primordia and begins to produce flower primordia (Frank 1996, Frank et al. 1997). Previously formed leaf buds continue to grow and develop (Esau 1960, Langer 1972). Many domesticated cool season grasses reach the three and a half new leaf stage around late April to early or mid May. Most native cool season grasses reach the three and a half new leaf stage around early June, and most native warm season grasses reach the three and a half new leaf stage around mid June (Manske 1999a).

Grass tillers exhibit short shoot and long shoot strategies of stem elongation. Grasses with short shoots do not produce significant internode elongation during vegetative growth and the apical meristem remains below grazing or cutting height. Production of new leaf primordia continues until the apical meristem changes to reproductive status and developing leaves continue to expand until the flower stalk elongates (Dahl 1995). Grasses with long shoots elevate the apical meristem a short distance above ground level by internode elongation while still in the vegetative phase (Dahl 1995). After the apical meristem has changed from vegetative status, additional stem elongation occurs during the sexual reproductive phase. Grass species with long shoot

tillers are nearly always decreased in pastures that are repeatedly grazed heavily (Branson 1953).

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

Recruitment of new grass plants developed from seedlings is negligible in healthy grassland ecosystems. The frequency of true seedlings is extremely low in functioning grasslands, and establishment of seedlings occurs only during years with favorable moisture and temperature conditions (Wilson and Briske 1979, Briske and Richards 1995), in areas of reduced competition from vegetative tillers, and when resources are readily available to the growing seedling. Vegetative tiller growth is the dominant form of reproduction in semiarid and mesic grasslands (Belsky 1992, Chapman and Peat 1992, Briske and Richards 1995, Chapman 1996, Manske 1999a) not sexual reproduction and the development of seedlings.

Vegetative secondary tillers develop from lead tillers by the process of tillering. A vegetative tiller is a shoot derived from growth of an axillary bud (Dahl 1995) and is a complete unit with roots, stem, and leaves. All young tillers are dependent on the lead tiller for carbohydrates until they have developed their own root systems and mature leaves (Dahl 1995). After secondary tillers become independent, they remain in vascular connection with other tillers of the grass plant (Moser 1977, Dahl and Hyder 1977, Dahl 1995). There are two types of tillering: crown tillers and rhizome or stolon

tillers. Crown tillers grow vertically close to the lead tiller and within the enveloping leaf sheath, and tend to have a tufted or bunch-type growth habit (Dahl and Hyder 1977, Dahl 1995). Rhizome tillers penetrate the enveloping leaf sheath and grow horizontally below the soil surface away from the lead tiller for a distance before beginning vertical growth. Rhizome growth may be either continuous, producing tillers at progressive intervals, or terminal, producing one tiller when the apex turns up and emerges from the soil (Dahl 1995). The rhizome type of tillering results in the spreading or creeping growth habit of sod-forming plants (Dahl and Hyder 1977, Dahl 1995). If the horizontal growth is aboveground, it is a stolon (Dahl 1995). Stolons have continuous growth and form tillers at progressive nodes (Dahl 1995). Grass plants can produce both crown tillers and rhizome tillers. Generally, one tiller growth type is produced by a grass species more than the other tiller type. However, the expressivity of tiller type can be influenced by several growth factors and environmental conditions, and can be manipulated by defoliation management (Manske 2011b).

Meristematic activity in axillary buds and the subsequent development of vegetative tillers is regulated by auxin, a growth-inhibiting hormone produced in the apical meristem and young developing leaves of lead tillers (Briske and Richards 1995). The physiological process by which the lead tiller exerts hormonal control over axillary bud growth is lead tiller (apical) dominance (Briske and Richards 1995). Tiller growth from axillary buds is inhibited indirectly by auxin, as the inhibiting hormone does not enter the axillary buds (Briske and Richards 1995). Auxin interferes with the metabolic function of cytokinin, a growth hormone (Briske and Richards 1995). Partial defoliation of young leaf material from grass tillers at phenological growth between the three and a half new leaf stage and the flower (anthesis) stage can stimulate vegetative growth of secondary tillers from axillary buds. Defoliation temporarily reduces the production of the blockage hormone, auxin (Briske and Richards 1994). This abrupt reduction of plant auxin in the lead tiller allows for cytokinin synthesis or utilization in multiple axillary buds, stimulating the development of vegetative tillers (Murphy and Briske 1992, Briske and Richards 1994). Several axillary buds develop into secondary tillers following partial defoliation of lead tillers at vegetative stages of phenological growth. Apparently, none of the developing secondary tillers have growth far enough advanced to take complete hormonal control over the other developing axillary buds (Manske 1996a).

Growth of several secondary tillers from axillary buds requires an abundant supply of carbon and nitrogen. The source of the carbon is not from stored carbohydrates, but from increased photosynthetic capacity of remaining mature leaves and rejuvenated portions of older leaves not completely senescent (Ryle and Powell 1975, Richards and Caldwell 1985, Briske and Richards 1995, Coyne et al. 1995). The quantity of leaf area required to provide adequate quantities of carbon is 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 (Millard et al. 1990, Ourry et al. 1990). A threshold quantity of 100 pounds per acre (112 kg/ha) of mineral nitrogen needs to be available to the partially defoliated grass tillers in order for full activation of the vegetative tiller production processes (Manske 2009a, 2010b, 2011d).

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

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

Fall tillers are produced by cool-season grasses during the winter hardening process that starts around mid August. Warm-season grasses produce fall tiller buds that remain at or below ground level until the next growing season. The age of the meristematic tissue that produces fall tillers

and fall tiller buds is one generation younger than the meristem that produced the lead tillers and secondary tillers. Secondary tillers with apical meristem remaining in the vegetative status, fall tillers, and fall tiller buds become the lead tillers and vegetative tillers during the subsequent growing season.

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

Rhizosphere Organisms

The rhizosphere is the narrow zone of soil around active roots of perennial grassland plants and is comprised of bacteria, protozoa, nematodes, springtails, mites, endomycorrhizal fungi (Elliot 1978, Anderson et al. 1981, Harley and Smith 1983, Curl and Truelove 1986, Whipps 1990, Campbell and Greaves 1990) and ectomycorrhizal fungi (Caesar-TonThat et al. 2001b, Manske and Caesar-TonThat 2003, Manske 2007). The activity of rhizosphere organisms increases along the trophic hierarchy, starting with the bacteria. This microflora trophic level lacks chlorophyll and has low carbon (energy) content. Bacteria are microscopic single celled saprophitic organisms that consume large quantities of soil organic matter and are one of the primary producers of the rhizosphere. Increases in biomass and activity of the bacteria elevates the concentration of carbon dioxide (CO_2) resulting in stimulation of activity in the other rhizosphere organisms. Protozoa are single-celled microorganisms that are mainly small amoeba and feed primarily on bacteria. Nematodes are a diverse group of small nonsegmented worms. Most nematodes feed primarily on bacteria or fungi, some feed on protozoa, and some eat other nematodes. Springtails are the most abundant insect in grassland soils and they travel among rhizosphere structures. Minute springtails ingest considerable quantities of soil organic matter in order to eat fungi and bacteria. Mites are small eight-legged arachnids that travel among rhizosphere structures and feed on fungi, nematodes, small insects, and other mites. Mites help distribute fungus spores and bacteria through the soil by carrying them on their exoskeleton. Endomycorrhizal fungi are the other primary producers of the rhizosphere and are achlorophyllous

saprophytes that live on dead organic matter and can not fix carbon because they lack chlorophyll. The bacteria and fungi are the microflora saprotrophic organisms at the bottom of the food chain and makeup the greatest biomass of the rhizosphere. Both bacteria and fungi contain high proportions of nitrogen in relation to their carbon content. The rhizosphere organisms of the microfauna trophic levels graze on bacteria or fungi and ingest greater quantities of nitrogen than they need for a balanced diet based on energy (carbon); the excess nitrogen is excreted as ammonium (NH_4). The primary symbiotic function of the endomycorrhizal fungi is to nitrify the ammonium (NH_4) excreted by rhizosphere organisms and convert it into nitrate (NO_3), which is a form of mineral nitrogen usable by grass plants. The elevated rhizosphere organism activity caused by the increase in available carbon compounds results in a greater quantity of organic nitrogen converted into mineral nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005).

Along with the improvement of ecosystem biogeochemical processes and the resulting increase in available mineral nitrogen, the increase of mycorrhizal fungi biomass and activity benefits other grassland ecosystem functions. Endomycorrhizal fungi develop arbuscules, vesicles, and hyphae within root tissue of the host plant (Harley and Smith 1983) and secrete adhesive polysaccharides that bond soil particles around grass roots forming the structural environment for rhizosphere organisms, and the adhesive polysaccharides bind soil into aggregates resulting in increased soil pore spaces, increased water holding capacity, and increased rooting depth. Endomycorrhizal fungi also move phosphorus, other mineral nutrients, and water to the plant roots for absorption (Moorman and Reeves 1979, Harley and Smith 1983, Allen and Allen 1990, Box and Hammond 1990, Marschner 1992, Koide 1993, Marschner and Dell 1994, Smith and Read 1997).

Ectomycorrhizal fungi develop a sheath around the root with hyphae that do not enter the tissue of the host plant (Harley and Smith 1983) and secrete large amounts of adhesive polysaccharides forming water-stable aggregates in soil that are water permeable but not water soluable, and the increased soil aggregation improves soil quality, increases soil oxygenation, increases water infiltration, and decreases erodibility (Caesar-TonThat and Cochran 2000, Caesar-TonThat et al. 2001a, Caesar-TonThat et al. 2001b, Caesar-

TonThat 2002, Manske and Caesar-TonThat 2003, Manske 2007).

Defoliation Resistance Mechanisms

The complex of mechanisms and processes connected with the extensive interactions of the biotic and abiotic ecosystem components collectively became the defoliation resistance mechanisms and biogeochemical processes (Manske 2011b). If any of the numerous processes do not function at potential level, the ecosystem does not produce at potential level. Management of rangeland ecosystems must meet the biological and physiological requirements of the biotic components and stimulate the biogeochemical processes that cycle the abiotic components.

Activation of the three primary defoliation resistance mechanisms requires proper timing of partial defoliation. The effects of defoliation are not simply the removal of herbage from grass plants (Langer 1963, 1972): foliage removal disrupts plant growth and photosynthesis, and defoliation also changes physiological processes in all parts of the plant; alters the plant community microclimate by changing light transmission, moisture relations, and temperature; and changes the soil environment, thereby affecting soil organism activity (Manske 2000a). Grass plants developed the defoliation resistance mechanisms in response to grazing during the period of coevoluation with graminivores (McNaughton 1979, 1983; Coleman et al. 1983; Briske 1991; Briske and Richards 1995; Manske 1999a, 2011b). The defoliation resistance mechanisms help grass tillers withstand and recover from partial defoliation by grazing. The three main resistance mechanisms are: compensatory internal physiological processes, internal vegetative production of secondary tillers from axillary buds, and external symbiotic rhizosphere organism activity (McNaughton 1979, 1983; Coleman et al. 1983; Ingham et al. 1985; Mueller and Richards 1986; Richards et al. 1988; Briske 1991; Murphy and Briske 1992; Briske and Richards 1994, 1995; Manske 1999a, 2011b).

Defoliation resistance mechanisms developed during the period of 30 to 20 mya as derivatives of the coevolution of grass plants, rhizosphere organisms, and large grazing mammalian graminivores following the cooling of the global climate in the Eocene that reduced forest ecosystems and increased grassland ecosystems. The defoliation resistance mechanisms are a complex assemblage of biogeochemical and physiological processes that involve intricate interactions among rhizosphere microorganisms, grass plants, and large grazing graminivores. Activation of these mechanisms provides important biological and physiological processes permitting native grasses to produce greater herbage biomass and to increase basal cover; these mechanisms also enable grass plants to replace lost leaf material, to restore disrupted physiological processes, and to vegetatively produce secondary tillers from axillary buds after partial defoliation by grazing. The defoliation resistance mechanisms function at variable levels of activation depending on the quantity of available mineral nitrogen in grassland ecosystem soil. When mineral nitrogen is available at 100 lbs/ac (112 kg/ha) or greater, the defoliation resistance mechanisms function at full activation (Manske 2011e). When mineral nitrogen is available at less than 100 lbs/ac (112 kg/ha), defoliation resistance mechanisms function at levels less than full activation (Manske 2009a, 2011d). In addition, the water (precipitation) use efficiency processes decrease in grass plants growing in ecosystems with less than 100 lbs/ac (112 kg/ha) available mineral nitrogen causing herbage biomass production to be reduced by 49.6% (Wight and Black 1972, 1979).

The quantity of available mineral nitrogen in grassland ecosystems is dependent on the rate of mineralization of soil organic nitrogen by rhizosphere organisms (Coleman et al. 1983). The larger the rhizosphere volume and microorganism biomass the greater the quantity of soil mineral nitrogen converted (Gorder, Manske, and Stroh 2004). Rhizosphere volume and microorganism biomass are limited by access to simple carbohydrate energy (Curl and Truelove 1986). Healthy grass plants capture and fix carbon during photosynthesis and produce carbohydrates in quantites greater than the amount needed for tiller growth and development (Coyne et al. 1995). Partial defoliation of grass tillers at vegetative phenological growth stages by large grazing graminivores causes greater quantities of exudates containing simple carbohydrates to be released from the grass tillers through the roots into the rhizosphere (Hamilton and Frank 2001). With the increase in availability of carbon compounds in the rhizosphere, the biomass and activity of the microorganisms increases (Anderson et al. 1981, Curl and Truelove 1986, Whipps 1990). The increase in rhizosphere organism biomass and activity results in greater rates of mineralization of soil organic nitrogen converting greater quantities of available mineral nitrogen (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005).

Mineral nitrogen available in quantities of 100 lbs/ac (112 kg/ha) or greater allow defoliated grass tillers full activation of the defoliation resistance mechanisms (Manske 2009a, 2011d, 2011e). Full activation of the compensatory internal physiological processes within grass plants accelerates growth rates of replacement leaves and shoots, increases photosynthetic capacity of remaining mature leaves, increases allocation of carbon and nitrogen, improves water (precipitation) use efficiency, and increases restoration of biological and physiological processes enabling rapid and complete recovery of partially defoliated grass tillers. Full activation of the asexual internal processes of vegetative production increases secondary tiller development from axillary buds and increases initiated tiller density during the grazing season. Full activation of the external symbiotic rhizosphere organism activity increases mineralization of mineral nitrogen, increases ecosystem biogeochemical cycling of essential elements, and improves belowground resource uptake competitiveness (Wight and Black 1972, 1979; McNaughton 1979, 1983; Coleman et al. 1983; Ingham et al. 1985; Mueller and Richards 1986; Richards et al. 1988; Briske 1991; Murphy and Briske 1992; Briske and Richards 1994, 1995; Manske 1999a, 2011b; Kochy and Wilson 2000).

Biogeochemical Processes

Biogeochemical processes are processes performed by soil microorganisms that renew the nutrient flow activities in ecosystem soils of renewable natural resources. Biogeochemical processes transform stored essential elements from organic forms into plant usable inorganic forms. Biogeochemical processes capture replacement quantities of lost or removed major essential elements of carbon, hydrogen, nitrogen, and oxygen with assistance from active live plants and transform the replacement essential elements into storage as organic forms for later use. Biogeochemical processes decompose complex unusable organic material into compounds and then into reusable essential elements. The quantity of biogeochemical processes conducted in renewable natural resource ecosystems determines the degree of ecosystem renewal and is dependant on the rhizosphere volume and soil microorganism biomass.

An evolutionary survival mechanism of grass plants in response to partial defoliation and the loss of leaf area as forage to grazing graminivores is the production of double the quantity of leaf biomass than needed for normal plant growth and maintenance (Crider 1955, Coyne et al. 1995). All of the aboveground herbage biomass produced by perennial grasses in a growing season represents about 33% of the total biomass produced. About 67% of the annual perennial grass biomass is produced belowground. About 50% of the aboveground biomass is expendable by the plant. About half of the expendable leaf material is removed as senescent leaves that are broken from the plant and fall to the ground as litter, or removed as leaf material consumed by wildlife or consumed and destroyed by grasshoppers and other insects. About half of the expendable leaf material, or 25% of the aboveground biomass is consumed by grazing livestock (Manske 2012b).

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

All of the nondigestible dry matter and most of the nutrients consumed by grazing graminivores are deposited on the ground as manure in a couple of days. Most of the nutrients consumed and used by graminivores for maintenance are returned to the ecosystem in the feces and urine. None of the herbage biomass dry matter produced during a growing season is removed by graminivores from the rangeland ecosystem. All of the essential elements contained in the belowground biomass and contained in the nonconsumed aboveground biomass stay in the ecosystem. Nearly all of the essential elements used in the annual production of herbage biomass and soil organism biomass are retained and recycled in the ecosystem. Recycling of retained ecosystem organic matter by soil microorganisms decomposes complex unusable material into compounds and then into reusable essential elements.

Some essential elements are lost or removed from the ecosystem as output. If the rangeland ecosystem is burned, almost all of the essential elements in the aboveground herbage are volatilized, and if the soil is dry, some of the belowground essential elements are also lost (Russelle 1992). The metabolic process of respiration in soil organisms, plants, livestock, wildlife, and grasshoppers results in a lose of some essential elements as carbon dioxide, water vapor, and heat energy. Some essential elements are removed from the ecosystem as weight biomass

produced by wildlife and grasshoppers. The essential elements transferred from grass plants to grazing livestock and used for animal growth are removed from the ecosystem (Gibson 2009).

The small proportion of the ecosystem essential elements that are lost or removed annually need to be replenished by capturing input essential elements from the surrounding environment through ecosystem processes. The biogeochemical processes associated with active live plants and soil microorganisms can capture replacement quantities for the lost major essential elements of carbon, hydrogen, nitrogen, and oxygen.

Atmospheric carbon dioxide (CO_2) is the ecosystem input source for carbon. Atmospheric carbon dioxide which composes about 0.03% of the gasses in the atmosphere, exists at concentrations of around 370 to 385 mg/kg and is not limiting on rangelands. The carbon dioxide is fixed with hydrogen from soil water during the plant process of photosynthesis which converts energy from sunlight into chemical energy and assimilates simple carbohydrates. Capturing energy by fixing carbon has a relatively low impact on the plant organisms that posses chlorophyll and has low biological costs to the ecosystem resources (Manske 2011b).

Soil water (H_2O) is infiltrated precipitation water and is the ecosystem input source for hydrogen. Soil water is absorbed through the roots and distributed throughout the plant within the xylem vascular tissue. When the rate of water absorption by the roots is less than the rate of water loss from transpiration through stomata openings, plant tissue develops water stress (Brown 1995). Plant water stress limits growth. In western North Dakota, the perennial plant growing season months have a long-term periodicity rate of water deficiency conditions at 32.7%, for a mean of 2.0 months with water deficiency per growing season (Manske et al. 2010).

Wet deposition of nitrogen oxides (NO, N_2O) following lightning discharges is the ecosystem input source for nitrogen (Manske 2009b). The source of nitrogen for plant growth is mineral nitrogen (NO_3, NH_4) converted from soil organic nitrogen by rhizosphere organisms. Low quantities of available soil mineral nitrogen below 100 lbs/ac (112 kg/ha) is the major limiting factor of herbage growth on rangelands (Wight and Black 1979) and limits productivity more often than low water on rangeland ecosystems (Tilman 1990). However, rangeland soils are not deficient of nitrogen. Most of the nitrogen is immobilized in the soil as organic nitrogen. Untilled rangeland soils contain about 3 to 8 tons of organic nitrogen per acre (Manske 2011a). Soil organic nitrogen must be mineralized by rhizosphere organisms to become plant usable mineral nitrogen. The quantity of rhizosphere organisms is the limiting factor in rangeland ecosystems low in mineral nitrogen. Biomass and activity of organisms in the rhizosphere are limited by access to energy from simple carbohydrates which can be exuded from grass lead tillers with partial defoliation by grazing graminivores when grass tillers are at vegetative growth stages. Transforming nitrogen from organic nitrogen to mineral nitrogen and back to organic nitrogen is complex and has a great impact on many organisms at multiple trophic levels and has high biological costs on the ecosystem resources (Manske 2011a, 2011b).

Carbon dioxide, water, and nitrogen oxides are the ecosystem input sources for oxygen. Atmospheric oxygen composes about 28% of the gasses in the atmosphere. The oxygen cycle between the biotic and abiotic components of the ecosystem is closely linked to the carbon cycle and the water, or hydrological, cycle. Oxygen is vital for all organisms that carry out aerobic respiration. Oxygen is not limiting on rangeland ecosystems.

Radiant light from the sun is the ecosystem input source for energy. Radiant energy from the sun is necessary for photosynthesis (Manske 2011c). Intensity of sunlight can be greatly reduced by shading from taller plants. Nondefoliated live and standing dead leaves of grasses reduce light penetration to a similar degree as shrubs, even through shrub leaves are flat and wide and grass leaves are erect and linear (Kochy 1999). The light levels penetrating the leaf canopy can be about 20% of the light levels above the canopy (Peltzer and Kochy 2001).

Failure of a rangeland ecosystem to replenish essential elements at quantities equal to or greater than the annual amount of essential elements lost or removed from the ecosystem inhibits ecosystem biogeochemical processes from functioning at potential levels causing incremental decreases in productivity and gradual degradation of the ecosystem.

Activation of Ecosystem Mechanisms and Processes

The ecosystem mechanisms and processes are activated with partial defoliation by grazing of grass lead tillers at vegetative growth stages. The

twice-over rotation grazing strategy is the biologically effective management practice that coordinates defoliation by grazing with grass phenological growth stages. Three to six rangeland pastures are grazed from early June until mid October, with each of the pastures grazed during two periods per growing season. Each pasture in a rotation system is grazed for 7 to 17 days during the first period. The first grazing period is the 45 day interval from 1 June to 15 July when native grass lead tillers are between the 3.5 new leaf stage and the flower stage; these are the vegetative growth stages of grass tiller development at which partial defoliation by grazing activates the defoliation resistance mechanisms and the ecosystem biogeochemical processes. Activation of these mechanisms and processes does not occur at any other period during a growing season (Manske 1999a). The length of grazing on each pasture during the first period is the same percentage of 45 days as the percentage of the total season's grazable forage contributed by each pasture (Manske 2000a). The second grazing period is the 90 day interval from mid July to mid October and each pasture is grazed for double the number of days that it was grazed during the first grazing period. Livestock are removed from native rangeland pastures in mid October, towards the end of the perennial grass growing season, in order to allow the carryover tillers to store carbohydrates and nutrients that will maintain plant processes over the winter. Most of the upright vegetative tillers on rangeland ecosystems during fall are carryover tillers and will resume growth during the next growing season as lead tillers. Grazing carryover tillers after mid October causes termination of a large proportion of the population resulting in greatly reduced herbage biomass production during subsequent growing seasons (Manske 2011b).