

Degradation and Biological Restoration of Mixed Grass Prairie Ecosystems

Llewellyn L. Manske PhD
Research Professor of Range Science
North Dakota State University
Dickinson Research Extension Center
Report DREC 12-3058

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

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

Mixed grass prairie communities are complex ecosystems consisting of numerous

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

Degradation from Traditional Grazing Practices

Ecosystem processes function at some degree less than potential level each growing season that grazing defoliation is managed with traditional practices that are based on grassland use as forage for livestock. Soon after the ecosystem processes fail to function properly, the belowground components begin to deteriorate. The native grass live root biomass decreases (Whitman 1974), the defoliation

resistance mechanisms within grass plants diminish, the ecosystem biogeochemical processes decline, and the competitiveness of grass plant resource uptake deteriorates (Manske 2011b).

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

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

The traditional grazing management practice of 4.5 month seasonlong is grazed at moderate stocking rates on native grasslands between early June and mid October and is moderately antagonistic to mixed grass prairie ecosystems. After 20 years, the plant communities had been degraded 23% and were

dominated by native grasses. The mean monthly grazing season live herbage biomass production was 1280 lbs/ac with 55.1% native grasses, 30.6% upland sedges, and 14.5% forbs. The rhizosphere volume was reduced to 67.6 ft³/ac (29.8% of potential volume) and the available mineral nitrogen was reduced to 76.7 lbs/ac (Manske 2011a) (table 1).

The traditional grazing management practice of 6.0 month seasonlong is grazed at slightly heavier than moderate stocking rates on native grasslands between mid May and mid November and is highly antagonistic to mixed grass prairie ecosystems. After 20 years, the plant communities had been degraded 38% and were dominated by native grasses. The mean monthly grazing season live herbage biomass production was 906 lbs/ac with 53.8% native grasses, 27.1% upland sedges, and 19.2% forbs. The rhizosphere volume was reduced to 49.8 ft³/ac (21.9% of potential volume) and the available mineral nitrogen was reduced to 61.6 lbs/ac (Manske 2011a) (table 1).

The traditional grazing management practice of long duration 7.0 to 8.0 month seasonlong is grazed at moderate stocking rates on native grasslands starting in early May and continuing until late December or until inclement weather prevents late season grazing and is severely antagonistic to mixed grass prairie ecosystems. After 75 years, the plant communities had been degraded 57% and were dominated by native grasses; woody plant cover had invaded only 0.03% of the grazed area. The aboveground vegetation consisted of 23.9% standing dead and litter and 76.1% live herbage biomass. The peak growing season live herbage biomass was 1719 lbs/ac with 10.3% invasive domesticated grasses, 64.0% native grasses, 15.7% upland sedges, and 10.1% forbs. The rhizosphere biomass was reduced to 154.7 kg/m³ (38.1% of potential weight) and the available mineral nitrogen was reduced to 42.4 lbs/ac (Manske and Schneider 2012a) (table 1).

The traditional grazing management practice of 4.0 month deferred, delays grazing until grass tillers are mature, is grazed at moderate to heavy stocking rates on native grasslands between mid July and mid November and is extremely antagonistic to mixed grass prairie ecosystems. After 50 years, the plant communities had been severely degraded 69%. The great loss of native grasses created large open spaces and the deferred grazed areas became dominated by Kentucky bluegrass, smooth brome grass, and western snowberry. Woody shrub cover had invaded greater than 50% of the area. The aboveground vegetation consisted of 32.5% standing

dead, 32.1% current year shrub growth, and 35.4% live herbage biomass. The peak growing season live herbage biomass was 891 lbs/ac with 20.7% invasive domesticated grasses, 25.5% native grasses, 25.2% upland sedges, and 28.6% forbs. The rhizosphere biomass was greatly reduced and the available mineral nitrogen was reduced to 31.2 lbs/ac (Manske 2007a, 2011a) (table 1).

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

Degradation from Nondefoliation

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

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

reduces native warm season grasses more than native cool season grasses. Introduced cool season domesticated grasses have lower light saturation points than native grasses, permitting domesticated grasses to live in low light conditions.

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

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

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

lead tillers at growth stages between the 3.5 new leaf stage and the flower stage is required to activate the defoliation resistance mechanisms.

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

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

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

The nitrogen allocated for grass growth can be mobilized from shoot and root tissue (Briske and Richards 1995) when the preferential source of mineral nitrogen recently converted from soil organic nitrogen by active rhizosphere organisms is low. Low quantities of available soil mineral nitrogen below

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

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

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

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

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

The nondefoliation management practice of complete rest from grazing removes large graminivores for longer than a decade and is extremely antagonistic to mesic mixed grass prairie ecosystems. After 13 years of nondefoliation, the plant communities at site #1 had been greatly

degraded 87%. The 82.0% loss of native grasses with short shoots and basal leaves created large open spaces and the nongrazed areas at site #1 became dominated by invasive smooth brome grass. The aboveground vegetation biomass consisted of 68.0% standing dead and litter and 32.0% live herbage. The mean nongrazed live herbage biomass was 1630 lbs/ac with 93.9% invasive domesticated grasses, 2.2% native grasses, 2.2% upland sedges, and 1.8% forbs. The rhizosphere biomass was reduced to 54.1 kg/m³ (13.3% of potential weight) and the available mineral nitrogen was greatly reduced (Manske and Schneider 2012b) (table 1).

The nondefoliation management practice of complete rest from grazing removes large graminivores for longer than a decade and is extremely antagonistic to mesic mixed grass prairie ecosystems. After 13 years of nondefoliation, the plant communities at site #2 had been greatly degraded 81%. The 39.9% loss of native grasses with short shoots and basal leaves created large open spaces and the nongrazed areas at site #2 became dominated by invasive Kentucky bluegrass. The aboveground vegetation biomass consisted of 63.6% standing dead and litter and 36.4% live herbage. The mean nongrazed live herbage biomass was 1645 lbs/ac with 64.8% invasive domesticated grasses, 3.3% native grasses, 22.9% upland sedges, and 9.0% forbs. The rhizosphere biomass was reduced to 78.0 kg/m³ (19.2% of potential weight) and the available mineral nitrogen was greatly reduced (Manske and Schneider 2012b) (table 1).

The long-term nondefoliation management practice of complete rest from grazing removes large graminivores for longer than multiple decades and is extremely antagonistic to xeric mixed grass prairie ecosystems. After 75 years of nondefoliation, the plant communities at long-term nongrazed areas had been degraded 61%. The 74.4% loss of native grasses with short shoots and basal leaves created large open spaces and the long-term nongrazed areas became dominated by invasive Kentucky bluegrass; woody plant cover had invaded 54.4% of the nongrazed area. The aboveground vegetation biomass consisted of 52.4% standing dead and litter and 47.6% live herbage. The mean nongrazed live herbage biomass was 1713 lbs/ac with 59.8% invasive domesticated grasses, 22.7% native grasses, 7.0% upland sedges, and 10.6% forbs. The rhizosphere biomass was reduced to 127.2 kg/m³ (31.3% of potential weight) and the available mineral nitrogen was reduced to 39.5 lbs/ac (Manske and Schneider 2012a) (table 1).

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

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

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

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

Following the reduction in grass plant resource competitiveness, establishment of shrubs can occur in degraded grasslands, which frequently starts as clumps (Li and Wilson 1998). The belowground resources previously used by the healthy robust grasses, but no longer consumed by the smaller, less vigorous degraded grasses, are taken up by the shrub plants resulting in proportional increases of biomass production (Kochy and Wilson 2000). After grass competition for belowground resources is reduced, shrub rhizome suckers can regain the faster growth rates and higher survival rates (Li and Wilson 1998) resulting in greater shrub stem densities. As shrub stem density increases, the competition shifts to primarily the aboveground resources of light; under these different degraded conditions, shrubs have the advantage and the grasses are strongly suppressed (Kochy and Wilson 2000).

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

greater degree of competitiveness than the ungrazed grasses.

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

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

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

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

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

Restoration from Biologically Effective Defoliation

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

The defoliation resistance mechanisms developed early during the coevolution of grass plants and grazing graminivores (McNaughton 1979, 1983; Coleman et al. 1983; Briske 1991; Briske and Richards 1995; Manske 1999) and are a complex assemblage of biogeochemical and physiological processes that involve intricate interactions among rhizosphere microorganisms, grass plants, and large grazing graminivores. Activation of these

mechanisms provides important biological and physiological processes permitting native grasses to produce greater herbage biomass and to increase basal cover; these mechanisms also enable grass plants to replace lost leaf material, to restore disrupted physiological processes, and to vegetatively reproduce secondary tillers from axillary buds after partial defoliation by grazing. The defoliation resistance mechanisms function at variable levels of activation depending on the quantity of available mineral nitrogen in grassland ecosystem soil. When mineral nitrogen is available at 100 lbs/ac or greater, the defoliation resistance mechanisms function at full activation. When mineral nitrogen is available at less than 100 lbs/ac, the defoliation resistance mechanisms function at levels less than full activation (Manske 2009). In addition, the water (precipitation) use efficiency processes decrease in grass plants growing in ecosystems with less than 100 lbs/ac available mineral nitrogen causing herbage biomass production to be reduced by 49.6% (Wight and Black 1972, 1979).

The quantity of available mineral nitrogen in grassland ecosystem soils is dependent on the rate of mineralization of soil organic nitrogen by rhizosphere organisms. The larger the rhizosphere volume and microorganism biomass, the greater the quantity of soil mineral nitrogen converted. Rhizosphere volume and microorganism biomass are limited by access to simple carbohydrates (Curl and Truelove 1986). Healthy grass plants capture and fix carbon during photosynthesis and produce carbohydrates in quantities greater than the amount needed for tiller growth and development (Coyné 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 Pflieger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005). Mineral nitrogen available in quantities of 100 lbs/ac or greater allows defoliated grass tillers full activation of the defoliation resistance mechanisms (Manske 2009). Full activation of the compensatory internal physiological processes within grass plants accelerates growth rates

of replacement leaves and shoots, increases photosynthetic capacity of remaining mature leaves, increases allocation of carbon and nitrogen, improves water (precipitation) use efficiency, and increases restoration of biological and physiological processes enabling rapid and complete recovery of partially defoliated grass tillers. Full activation of the asexual internal processes of vegetative reproduction increases secondary tiller development from axillary buds and increases initiated tiller density during the grazing season. Full activation of the external symbiotic rhizosphere organism activity increases mineralization of mineral nitrogen, increases ecosystem biogeochemical cycling of essential elements, and improves belowground resource uptake competitiveness (Wight and Black 1972, 1979; McNaughton 1979, 1983; Coleman et al. 1983; Ingham et al. 1985; Mueller and Richards 1986; Richards et al. 1988; Briske 1991; Murphy and Briske 1992; Briske and Richards 1994, 1995; Manske 1999, 2011b; Kochy and Wilson 2000). Restoration of plant community vegetation composition lags behind restoration of ecosystem processes.

Restoration of degraded mixed grass prairie ecosystems dominated by native grasses can be accomplished by implementation of the twice-over rotation system which is a biologically effective grazing management strategy that coordinates defoliation events with grass phenological growth stages, meets the biological requirements of the plants and soil organisms, and meets the nutritional requirements of the grazing animals. After 20 years, the plant communities had been restored 100% with fully functioning defoliation resistance mechanisms, ecosystem biogeochemical processes, and resource uptake competitiveness. The mean monthly grazing season live herbage biomass production was 1794 lbs/ac with 74.7% native grasses, 14.2% upland sedges, and 11.1% forbs. The rhizosphere volume was increased to 227.1 ft³/ac and the biomass increased to 406.4 kg/m³ (100.0% of potential volume and biomass) and the available mineral nitrogen was increased to 177.8 lbs/ac (Manske 2007b, 2011a) (table 1).

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

upland sedges, and 1.8% forbs. The rhizosphere biomass was reduced to 54.1 kg/m³ (13.3% of potential weight) and the available mineral nitrogen was greatly reduced. After 6 years of twice-over rotation grazing management, the plant communities at site #1 had been restored about 41%. The aboveground vegetation biomass consisted of 35.6% standing dead and litter and 64.4% live herbage. The mean live herbage biomass was 2447 lbs/ac with 89.6% domesticated grasses, 3.5% native grasses, 2.0% upland sedges, and 4.9% forbs. The rhizosphere biomass had increased to 167.1 kg/m³ (41.1% of potential weight) and the available mineral nitrogen had increased to 59.9 lbs/ac (Manske and Schneider 2012b) (table 1).

Restoration of degraded mesic mixed grass prairie ecosystems at site #2 dominated by Kentucky bluegrass was attempted by implementation of the twice-over rotation system. Before the grazing treatment started, the aboveground vegetation biomass consisted of 63.6% standing dead and litter and 36.4% live herbage. The mean live herbage biomass was 1645 lbs/ac with 64.8% invasive domesticated grasses, 3.3% native grasses, 22.9% upland sedges, and 9.0% forbs. The rhizosphere biomass had been reduced to 78.0 kg/m³ (19.2% of potential weight) and the available mineral nitrogen was greatly reduced. After 6 years of twice-over rotation grazing management, the plant communities at site #2 had been restored about 53%. The aboveground vegetation biomass consisted of 39.3% standing dead and litter and 60.7% live herbage. The mean live herbage biomass was 2174 lbs/ac with 58.0% domesticated grasses, 26.1% native grasses, 11.3% upland sedges, and 4.6% forbs. The rhizosphere biomass had increased to 214.3 kg/m³ (52.7% of potential weight) and the available mineral nitrogen had increased to 56.7 lbs/ac (Manske and Schneider 2012b) (table 1).

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

for invasion of undesirable introduced domesticated grasses (Manske and Schneider 2012b).

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

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

and Schneider 2012a). Antagonistic management practices have caused the abundant shrub cover greater than 5% on the regions upland landscapes.

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

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

Fire has been an environmental factor on mixed grass prairie as lightning-set fires and Indian-set fires. Spring burns result in great quantities of shrub sucker stems, and lost carbohydrate stores can be completely replenished by the new plant material in one growing season. August fires remove all or most of the top growth of shrubs and result in fewer sucker shoots the following year than spring burns. When the soil is not dry, prescribed burns during August cause the least damage to native cool season and warm season grasses and perennial forbs. The belowground rhizomes and crown stem bases are

usually not damaged by fire because of the protection provided by soil. Some of the buds on the belowground parts develop into new aerial sucker stems. Prescribed burning alone will not remove deciduous shrubs that can reproduce vegetatively from the northern mixed grass prairie (Manske et al. 2006a, Manske 2007a, 2011a).

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

Chemical management control of shrubs requires termination of the regenerative capabilities of the rhizomes and the crown stem bases by disabling the meristematic tissue. Foliage-active herbicides must enter the leaf tissue through the stomata openings or penetrate the outer cuticle layer, be absorbed through leaf tissue by diffusion, moved to the vascular system within the leaf, and be translocated from the leaves downward through the phloem vascular system to the metabolically active sites of the crowns and rhizomes. During rapid stem

elongation, nonstructural carbohydrates move from the storage sites in the rhizomes and the crowns upward through the phloem vascular system to the active growing points of the stem preventing downward movement of herbicides. As leaf area increases and carbohydrate production by photosynthesis exceeds the demands for growth, the surplus carbohydrates are moved downward through the phloem for storage in the rhizomes and crowns (Coyne et al. 1995); downward translocation of herbicides could occur at that time if the herbicides were in the leaf tissue. However, as leaves mature, they develop a thick cuticle layer and dense cell walls reducing herbicide penetration and absorption. Most shrubs have a brief vulnerable stage when the herbicide plus surfactant penetration into leaf tissue is decreasing and herbicide translocation downward is increasing. For many shrubs this short period occurs from about 10 June until 20 June.

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

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

Recapitulation

Mixed grass prairie ecosystems are complex and consist of numerous biotic and abiotic components that function together through three primary processes; the defoliation resistance mechanisms, the ecosystem biogeochemical processes; and the plant resource uptake processes. When these three primary processes do not function at potential level, the ecosystem does not function at potential level. Partial defoliation by grazing

graminivores is required to trigger activation of the primary processes and the quantity of available soil mineral nitrogen and the quantity of available fixed carbon affect the level at which the primary processes function. Fully functioning processes require mineral nitrogen to be available at 100 lbs/ac or greater and require the quantity of carbon fixed through photosynthesis from 75% to 67% of the leaf area of grass lead tillers prior to peak live herbage biomass and from 50% of the leaf area post peak biomass.

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

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

Restoration of degraded mixed grass prairie ecosystems requires returning the three primary ecosystem processes back to functioning at potential levels. The rhizosphere organism biomass must be improved initially to increase mineralization of nitrogen and other essential elements. Rhizosphere organisms are limited by access to energy in the form of short carbon chains. Exudation of short carbon chain energy can be released from the grass lead tillers through the roots into the rhizosphere by removal of 25% to 33% of the aboveground leaf biomass by large grazing graminivores when the lead tillers are between the 3.5 new leaf stage and the flower stage. As a result of this successful initial recovery of the biogeochemical processes, the amounts of available mineral nitrogen, essential elements, fixed carbon, and soil water start increasing from deficient quantities towards functional quantities. With the increasing component resources, native grass plants are able to synthesize increasing

quantities of carbohydrates, proteins, and nucleic acids. Activation of the defoliation resistance mechanisms provides important biological and physiological processes permitting native grasses to use the vital organic compounds in increasing quantities for the production of herbage biomass and basal cover. With implementation of the belowground resource uptake of soil water, mineral nitrogen, and other essential elements, the native grasses become more competitive. The symptoms of improving changes in the vegetation lag behind the improving changes in the functionality of the primary processes.

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

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

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

Acknowledgment

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

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

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

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