

Discussion

Removal of cattle grazing does not promote development of stable climax plant communities and does not preserve prairie grasslands in perpetuity.

Mixed grass prairie communities deprived of large grazing animals decline steadily into unhealthy disfunctional ecosystems with severe reductions of native grasses, considerable decreases of desirable forbs, enormous increases of introduced domesticated grasses, remarkable increases of woody shrubs and trees, and excessive increases of standing dead and litter as a result of diminished grass plant defoliation resistance mechanisms, degraded ecosystem biogeochemical processes, and low grass plant resource uptake competitiveness. Activation of the defoliation resistance mechanisms, the ecosystem biogeochemical processes, and grass resource competitiveness requires partial defoliation by large grazing herbivores (graminivores). Grazing animals are essential annual growing season components of rangeland ecosystems.

Traditionally, rangeland ecosystems have been managed from the perspective of the “use” of the grassland. Livestock grazing along with watershed, wildlife, and recreation were considered to be the major uses. Management of rangelands from the perspective of a single use or for multiple uses narrowly considers only a few ecosystem components directly related with these primary uses or products removed. Management for a use does not consider rangelands as complex ecosystems and neglects to address the needs of all other ecosystem components. Management of rangelands for a use, no matter how noble, results in degradation of the ecosystems. The uses of rangeland resources should not be the objective of management. The management should be the means to accomplish the uses. Management strategies need to be designed to beneficially stimulate all ecosystem components to function at potential levels.

Rangelands 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. Rangeland ecosystems are functioning units of coacting biotic organisms interacting with the abiotic components and the environment. The complex of mechanisms and processes connected with these extensive interactions have been identified as defoliation resistance mechanisms and biogeochemical processes. If any of the numerous processes are not functioning at potential level, the ecosystem does not function at potential level. Management of rangeland ecosystems needs to meet the biological and physiological requirements of the biotic components and stimulate the biogeochemical processes that cycle the abiotic components. Mixed grass prairie communities require biologically effective partial defoliation by annually managed grazing animals in order to persist as healthy and productive ecosystems. Thus, providing the means to accomplish the uses of watershed, wildlife habitat, recreation, and livestock forage at the same time on fully functional rangeland ecosystems.

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 (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 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).

Biologically effective grazing management strategies have 4.5 month grazing seasons on native grasslands between early June and mid October with 2 grazing periods in each of the 3 to 6 pastures and the rotation dates coordinate partial defoliation by grazing with grass phenological growth stages. Removal of about 25% to 33% of the aboveground leaf material of grass lead tillers between the 3.5 new leaf stage and the flower stage increases the quantity of carbon exudates released through the roots into the rhizosphere, enlarges the rhizosphere volume to 227.06 ft³/ac, increases rhizosphere biomass to 552.80 tons/ac, and raises rates of mineralization of soil organic nitrogen into mineral nitrogen to 177.84 lbs/ac (Manske 2009, 2011b). The partially defoliated grass tillers in grassland ecosystems with abundant quantities of available mineral nitrogen respond positively to grazing because the defoliation resistance mechanisms function at the high levels of full activation that results in complete recovery of defoliated tillers replacing leaf and stem material at greater quantities than that removed by grazing, increasing total tiller density and herbage production, and fully restoring, and then maintaining, the biogeochemical processes and the health of the grassland ecosystem (Manske 2009, 2010b, 2011a).

Traditional grazing management practices with 4.5 month grazing seasons on native grasslands between early June and mid October, but with no rotation dates or rotation dates that are not coordinated with grass phenological growth stages cause slow deterioration of the ecosystems. The antagonistic grazing defoliation results in decreases in the quantities of carbon exudates released through the roots into the rhizosphere, reducing the rhizosphere

volume to 67.61 ft³/ac, decreasing the organism biomass and activity, and reducing the rates of mineralization of soil organic nitrogen into mineral nitrogen to 76.70 lbs/ac. The grazed grass tillers in grassland ecosystems with deficient quantities of available mineral nitrogen respond negatively to grazing because the defoliation resistance mechanisms function at reduced levels of less than full activation that results in incomplete recovery of grazed tillers replacing less leaf and stem material than the quantity removed by grazing decreasing total tiller density and herbage production, and causing a slow steady decline in the biogeochemical processes and the grassland ecosystem health (Manske 2011a).

Traditional grazing management practices with 6.0 month grazing seasons on native grasslands starting before early June and continuing past mid October, and no rotation dates or rotation dates that are not coordinated with grass phenological growth stages are harmful to the perennial native grass plants, the rhizosphere organisms, and the ecosystem biogeochemical processes. This highly antagonistic defoliation by grazing causes reductions in the quantity of plant carbon exudation through the roots into the rhizosphere. The rhizosphere volume diminishes greatly to 49.75 ft³/ac, reducing the organism biomass and activity, and decreasing the quantities of soil organic nitrogen converted into mineral nitrogen to 61.61 lbs/ac. The grazed grass tillers in grassland ecosystems with insufficient quantities of mineral nitrogen respond negatively to grazing because the defoliation resistance mechanisms and biogeochemical processes are activated at extremely low levels (Manske 2009, 2010a) and plant recovery from grazing is incomplete with limited amounts of leaf and stem material replaced, decreasing grass tiller density and herbage production greatly, and causing deterioration in the grassland ecosystem health (Manske 2011a).

Developed grazing management practices with 4.0 month grazing seasons on a deferred native grassland pasture between mid July and mid November that, by design, delays grazing until grass tillers are mature with most producing seeds. This extremely antagonistic grazing defoliation suppresses the amount of carbon exudates released through the roots into the rhizosphere, shrinking the rhizosphere volume and organism biomass, and reducing the rates of mineralization of soil organic nitrogen into mineral nitrogen to 31.20 lbs/ac. The grazed grass tillers in grassland ecosystems with inadequate quantities of mineral nitrogen respond negatively to grazing because the defoliation resistance mechanisms and biogeochemical processes barely function. Tiller

development and herbage biomass production are extremely low. Numerous undesirable plants invade the native communities and the grassland ecosystem health degrades to low condition (Manske 2011a).

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.

Seventy five years ago, the healthy native grass communities in the four reference area exclosures started to deteriorate as a result of withholding grazing by large graminivores. Soon after grazing graminivores had been removed from the grasslands, the native grass live root biomass decreased (Whitman 1974), standing dead leaves and litter accumulated (Brand and Goetz 1986), and ecosystem biogeochemical processes declined (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. Without partial defoliation by grazing, only a small quantity of short carbon chain energy leaks from the grass roots into the rhizosphere; this low amount of simple carbon compounds is barely enough to sustain a small 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. Termination of annual partial defoliation by graminivores depletes these substantive processes resulting in deficiencies in mineral nitrogen and other essential elements.

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 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 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 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 leaf tillers with partial defoliation by grazing graminivores when grass tillers are at vegetative growth stages. 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 to slow leakage into the rhizosphere, 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).

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, 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. 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, remarkable increases of woody shrub and tree species, and degradation of range condition to very low percentages of potential climax vegetation after 75 years.

A remarkably high quantity of woody shrub and tree species and an exceptionally great number of individual woody plants were able to develop on the four reference area ungrazed exclosures 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 reduction of the competitiveness of the grasses for belowground resources of mineral nitrogen and soil water in conjunction with diminution of the defoliation resistance mechanisms and degradation of the biogeochemical processes in the grass plant communities that resulted from the antagonistic nondefoliation management practices fully explains the extraordinary increase of woody shrubs and trees growing in the four ungrazed exclosures.

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 grazed areas and the ungrazed exclosures of the four reference areas have all had at least 75 years without fire defoliation. However, if fire suppression had caused the increase of shrubs and trees, the quantity of woody plants would have been nearly similar on the ungrazed and grazed areas. The ungrazed exclosures have had a far greater intrusion of woody plants than the grazed areas. The grazed grasses have maintained a greater degree of competitiveness than the ungrazed grasses. The greater increase of woody plants into the grass communities of the ungrazed exclosures has not been the result of fire suppression. The increased woody plant infestation of the exclosures has been caused by the greatly reduced competitiveness of the ungrazed grasses and the degradation of the biogeochemical processes in the grass plant communities that resulted from the removal of partial defoliation by large grazing graminivores.

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 Koehy 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 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.

Had the early grassland ecologists known about the conclusions from the grass-shrub competition research conducted at the University of Regina and understood the defoliation resistance mechanisms and the biogeochemical processes, it would appear extremely plausible that the conjectural observations of increasing shrubs and trees and undesirable forbs and grasses in grassland communities that were explained as results of fire suppression, would have been scientifically explained as shrubs and trees and introduced forbs and grasses effectively competing for a portion of the belowground resources of nutrients and soil water after the competitiveness of the grasses had been reduced as a result of degradation of the grass community caused by antagonistic management practices. The key to woody shrub and tree and herbaceous plant control in grass 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.

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