Restoration of Degraded Prairie Ecosystems

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All prairie ecosystems that are not functioning at potential biological levels are degraded by some degree. Degradation of prairie ecosystems is caused by management practices that are antagonistic to the defoliation resistance mechanisms in perennial grasses. Restoration of degraded prairie ecosystems requires that managers understand the defoliation resistance mechanisms within grass plants, the symbiotic rhizosphere organisms' relationship with ecosystem biogeochemical processes, and the activation of these processes with defoliation by grazing animals.

Grass plants and large grazing herbivores evolved together. During the coevolutionary period, grasses developed biological processes that help plants withstand and recover from defoliation by grazing (Manske 2000a, 2007). Collectively, these processes are the Defoliation Resistance Mechanisms (McNaughton 1979, 1983; Coleman et al. 1983; Briske 1991; Briske and Richards 1995; Manske 1999). These mechanisms are: compensatory physiological processes within grasses (McNaughton 1979, 1983; Briske 1991); vegetative reproduction of secondary tillers from axillary buds (Mueller and Richards 1986; Richards et al. 1988; Murphy and Briske 1992; Briske and Richards 1994, 1995); and symbiotic rhizosphere organism activity (Coleman et al. 1983, Ingham et al. 1985). The defoliation resistance mechanisms accelerate growth rates of replacement leaves and shoots, increase photosynthetic capacity of remaining mature leaves, increase allocation of carbon and nitrogen, increase secondary tiller development from axillary buds, and increase conversion of soil organic nitrogen into plant usable mineral nitrogen.

Defoliation by grazing that removes 25% to 33% of the leaf area of perennial grass tillers at phenological growth stages between the three and a half new leaf stage and the flower (anthesis) stage is needed to trigger these beneficial mechanisms (Manske 1999, 2007), however, a threshold quantity of 100 pounds per acre or greater of mineral nitrogen processed by the rhizosphere organisms is required for full activation of the defoliation resistance mechanisms in grazed grass tillers (Manske 2009, 2010).

Perennial grass plants and rhizosphere organisms interact in the narrow zone of soil around grass roots. The rhizosphere contains bacteria, protozoa, nematodes, mites, springtails, and endomycorrhizal fungi (Elliot 1978, Anderson et al. 1981, Harley and Smith 1983, Curl and Truelove 1986, Whipps 1990, Campbell and Greaves 1990). The grass plants release carbon compounds (Campbell and Greaves 1990), including sugars, through the roots into the rhizosphere, and the soil microorganisms release mineral nitrogen that the plants absorb (Ingham et al. 1985, Clarholm 1985, Biondini et al. 1988, Frederick and Klein 1994, Frank and Groffman 1998). The endomycorrhizal fungi also provide phosphorus, other mineral nutrients, and water that the plant needs for growth (Moorman and Reeves 1979, Harley and Smith 1983, Allen and Allen 1990, Koide 1993, Marschner and Dell 1994, Smith and Read 1997). Activity of the soil microorganisms increases with the availability of carbon compounds in the rhizosphere (Curl and Truelove 1986, Whipps 1990), and the elevated microorganism activity results in an increase in mineral nitrogen available to the grass plant (Coleman et al. 1983, Klein et al. 1988, Burrows and Pfleger 2002, Rillig et al. 2002, Bird et al. 2002, Driver et al. 2005).

Grazing lead tillers between the three and a half new leaf stage and the flower stage (Manske 1999) increases the quantity of carbon compounds the defoliated plants release into the rhizosphere (Hamilton and Frank 2001). The increase in mineral nitrogen produced by elevated rates of microorganism activity allows the plant to accelerate growth and recover more quickly from defoliation. This beneficial activity does not occur when grazing is conducted during the middle and late growth stages of grass plants (Manske 2000a, 2007).

The cause of degradation of prairie ecosystems is antagonistic management practices that are not coordinated with plant phenological growth stages and do not meet the biological requirements of the perennial grass plants and the rhizosphere organisms. Ecosystem deterioration starts with management caused reductions in the quantity of plant carbon exudates released into the rhizosphere;

reduced carbon exudates causes a decrease in rhizosphere organism biomass and activity; reduced rhizosphere organism vitality causes a reduction in the quantity of soil organic nitrogen converted into mineral nitrogen. Decreases in the amount of available mineral nitrogen in the ecosystem causes reductions in grass herbage biomass production and causes decreases in plant density (basal cover). When the quantity of mineral nitrogen drops below 100 pounds per acre, the defoliation resistance mechanisms fail to be activated and plant recovery from grazing is incomplete (Manske 2009, 2010). In addition, the water use efficiency processes cease 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). As degradation continues, numerous large bare spaces between grass plants are created in the plant community. These open spaces are ideal habitat for growth of opportunistic "weedy" plant species. 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 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.

The greatest antagonistic effects to prairie ecosystems occur from long-term nondefoliation (idle) management that withholds defoliation from a grassland ecosystem. Nondefoliation management results in an accumulation of standing dead leaves that shade lower leaves, increasing the rate of leaf senescence and reducing the rate of photosynthesis, that causes a decrease in the supply of carbohydrates, resulting in a reduction in growth of new leaves and roots (Langer 1972, Briske and Richards 1995). Shading increases grass tiller mortality and reduces grass density (Grant et al. 1983). Reduction of root biomass (Whitman 1974, Brand and Goetz 1986) reduces active root length for interaction with rhizosphere organisms and causes a decrease in absorption of water and nutrients from the soil. Lack of defoliation greatly reduces the quantity of plant carbon exudated into the rhizosphere reducing organism biomass and activity causing a reduction in conversion of soil organic nitrogen into mineral nitrogen.

Under nondefoliation management, dead leaves remain standing for several years. Standing dead plant material not in contact with soil does not decompose through microbial activity. The dead material breaks down slowly as a result of leaching and weathering. A thick mulch layer builds up that modifies soil temperatures, inhibits water infiltration, and retains increasing portions of ecosystem nutrients reducing the quantities of soil organic carbon and nitrogen. Reduced sunlight from shading and reduced quantities of hydrogen, carbon, and nitrogen in the soil, severely reduces the rates of nutrient cycles and biogeochemical processes causing further reductions in leaf growth, tiller leaf area, and grass herbage biomass production. Plant community degradation by nondefoliation promotes changes in composition towards increases in shade-tolerant and shade-adapted replacement species (Manske 2008a).

Prairie ecosystems consist of three components: grass plants, rhizosphere microorganisms, and large grazing herbivores. All three components must be present at sufficient quantities in order for the ecosystem biogeochemical processes to function properly during each growing season. Removal of the large herbivores for one growing season starts the degeneration processes. Degradation of prairie ecosystems caused by nondefoliation management occurs slowly, however, the degree of deterioration to ecosystem biogeochemical processes and plant community structure descends magnitudes greater than any degradation caused by antagonistic grazing management practices (Manske 2008a).

Traditional grazing management practices that are not coordinated with plant phenological growth stages and do not meet the biological requirements of the perennial grass plants and the rhizosphere organisms are detrimental to prairie ecosystems. The deferred grazing, 6.0 month seasonlong, and 4.5 month seasonlong management strategies are antagonistic to rhizosphere organism activity, ecosystem biogeochemical processes, and the nitrogen cycle by causing retardation in the quantity of plant carbon exudation into the rhizosphere. The rhizosphere volume diminishes to levels with insufficient organism biomass and activity to convert soil organic nitrogen into available mineral nitrogen at the threshold rates of 100 lbs/ac. The low rhizosphere volume on the deferred grazing strategy converts an extremely low quantity of mineral nitrogen at 31.2 lbs/ac. The low rhizosphere volume of 49.8 ft^3/ac on the 6.0-m seasonlong grazing strategy converts a low quantity of mineral nitrogen at 62.0 lbs/ac. The low rhizosphere volume of 67.6

ft^3/ac on the 4.5-m seasonlong grazing strategy converts a low quantity of mineral nitrogen at 76.7 lbs/ac (Manske 2008b). The defoliation resistance mechanisms are not activated on prairie ecosystems managed with traditional grazing practices that process mineral nitrogen at rates less than 100 lbs/ac, even if the grass tillers are defoliated at the proper phenological growth stages (Manske 2009, 2010). Without help from compensatory physiological processes and from vegetative reproduction of secondary tillers from axillary buds, desirable native grass tillers cannot fully recover from defoliation by grazing; the grass density and grass herbage biomass production progressively decrease and less desirable replacement species backfill as open spaces develop.

Management strategies that defer grazing until after the flowering stage were intended to enhance sexual reproduction and increase the quantity of seeds produced. However, deferred grazing causes a decrease in native grass plant density (Sarvis 1941, Manske et al. 1988). Most young grass plants in grassland ecosystems start not as seedlings but as vegetative tillers that grow from axillary buds on the crowns of an established plant. These vegetative tillers make up the majority of the plant population because they have a competitive advantage over seedlings. Tillers initially draw support from the root systems of parent tillers, while seedlings must rely on their own less-developed structures.

Tiller development from axillary buds is regulated by lead tillers (Briske and Richards 1995), through a process called lead tiller dominance. The lead tillers produce an inhibitory hormone that prevents the growth hormone from activating growth within axillary buds (Briske and Richards 1995). Reduction of the amount of the inhibitory hormone in the plant allows the growth hormone to activate cell growth in multiple axillary buds (Briske and Richards 1994). With that inhibitory hormone reduced, the growth hormone stimulates vegetative reproduction (Murphy and Briske 1992, Briske and Richards 1994), and secondary tillers develop from the axillary buds (Langer 1972). Grazing that removes 25% to 33% of the young leaf tissue from the aboveground portion of lead tillers after the three and a half new leaf stage and before the flower stage increases activation of vegetative tillers from axillary buds (Manske 2007).

All grass species in the Northern Plains have strong lead tiller dominance except Kentucky bluegrass and meadow bromegrass, which have low levels of inhibitory hormones and relatively higher levels of tiller development. Plants with these growth characteristics have greater demand for water than grasses with strong lead tillers and cease growth processes during minor water deficiency periods.

Beneficial grass plant response to grazing depends on the timing of defoliation. Grazing grass plants prior to the three and a half new leaf stage negatively affects grass growth (Manske 2000b). Early seasonal growth of grass plants depends on carbohydrates stored in the roots, rhizomes, and stem bases (Trlica 1977), and prematurely grazed plants are unable to replenish adequate amounts of carbohydrates to support active growth (Coyne et al. 1995, Manske 1999). Grazing after the three and a half new leaf stage and before the flower stage allows plants to establish sufficient leaf area to produce adequate photosynthetic assimilates to meet leaf growth requirements and allows all leaf bud primordia in the apical meristem to develop into leaf buds (Manske 1999).

If no defoliation occurs before the flower stage, as on a deferred grazing strategy, the lead tiller inhibits vegetative tiller development until the inhibitory hormone production naturally declines during the flower stage. This hormone reduction permits one axillary bud to grow and develop into a secondary tiller, which in turn produces inhibitory hormones that prevent growth of the other six to eight axillary crown buds (Mueller and Richards 1986). These dormant axillary buds are never activated and become senescent with the lead tiller. The lack of defoliation of lead tillers prior to the flower stage diminishes recruitment of vegetative tillers, leading to decreased plant density and reduced rhizosphere organism activity; this reduction results in decreased conversion of soil organic nitrogen into mineral nitrogen. No evidence has been found to suggest that grazing the lead tiller after it has reached the flower stage has beneficial stimulatory effects on vegetative tiller development or rhizosphere organism activity (Manske 2000a).

Late season grazing after mid October and early season grazing before the three and a half new leaf stage are antagonistic to native perennial grasses. Late grazing is not harmful to senescent lead tillers that produced seeds that growing season. Usually around 25% of the tiller population reaches the reproductive phenological growth stage, however, it can vary from 5% to 50% of the tiller population. The other tillers that did not produce seeds will overwinter and resume active growth during the subsequent growing season. Late season grazing of carryover tillers causes decreased tiller numbers, reduced total basal area, and reduced quantities of herbage biomass produced (Olson and Richards 1988, Coyne et al. 1995). Winter survival of carryover tillers depends on having adequate carbohydrate reserves which is closely related to the amount of active leaf material remaining on each tiller during the winter hardening process, that occurs between mid August and mid October. The crown, portions of the root system, and some leaf tissue remain active and maintain physiological processes throughout the winter using stored carbohydrates. Depletion of the carbohydrates reserves before spring causes tiller death, “winter kill”.

During early spring, portions of the carryover tillers’ leaves from the previous year that have intact cell walls regreen with chlorophyll and provide crucial photosynthetic product for new leaf growth (Briske and Richards 1995). New growing leaves draw carbohydrates from the carryover older leaves until maintenance and growth requirements can be met by the new leaves (Langer 1972, Coyne et al. 1995). Removal of leaf matreial by grazing from grass tillers not yet at the three and a half new leaf stage deprives the new tillers of foliage needed for photosynthetic product and causes a demand on the low levels of carbohydrate reserves that results in a reduction of the herbage biomass production well below potential quantities later in the growing season (Campbell 1952, Rogler et al. 1962, Manske 2000b).

The twice-over rotation grazing management system is the biologically effective management strategy that is coordinated with grass phenological growth stages and meets the biological requirements of the perennial grass plants and soil organisms by applying defoliation treatment to grass plants at the appropriate growth stages that activate the defoliation resistance mechanisms and stimulate the symbiotic rhizosphere microorganisms biomass and activity (Manske 1999, 2000a; Gorder, Manske, Stroh 2004). The increased rhizosphere activity results in an increased quantity of available mineral nitrogen. The high rhizosphere volume of 227.1 ft^3/ac on the twice-over rotation grazing strategy converts a high quantity of mineral nitrogen at 177.8 lbs/ac (Manske 2009, 2010).

The twice-over rotation grazing management system uses three to six pastures. Every pasture is grazed during two periods per growing season. Each pasture is grazed for 7 to 17 days during the first period, the 45-day interval from 1 June to 15 July. The length of the first period on each pasture is the same percentage of 45 days as the percentage of the total season's grazeable forage each pasture contributes (Manske 2000a). During the second period, after mid July and before mid October, each pasture is grazed for double the number of days it was grazed during the first period. Livestock are removed in mid October.

The coordinated defoliation improves plant health and stimulates biological and ecological processes within grass plants and the ecosystem so that beneficial changes to plant growth, soil organisms, and biogeochemical cycles in the ecosystem result (Manske 2000a). During the first grazing period, grasses are between the three and a half new leaf and flower stages, the stages of plant development at which grazing stimulates the defoliation resistance mechanisms that increase tillering from axillary buds and enhance rhizosphere organism activity increasing the conversion of soil organic nitrogen into mineral nitrogen. Increased vegetative reproduction by tillering contributes to the development of greater plant basal cover and to the production of greater grass herbage weight; increased activity of the soil organisms in the rhizosphere supplies the plant with greater quantities of nutrients to support additional growth (Manske 2000a).

Restoration of degraded prairie ecosystems requires implementation of a biologically effective grazing management strategy that meets the biological requirements of the perennial grass plants and rhizosphere organisms, and that is coordinated with perennial grass phenological growth stages. Proper defoliation during the first grazing period removes 25% to 33% of the leaf area of grass tillers between the three and a half new leaf stage and the flower stage. This defoliation by grazing treatment increases the quantity of plant carbon exudates released into the rhizosphere causing an increase in the biomass and activity of the rhizosphere organisms that results in an increase in the quantity of soil organic nitrogen converted into mineral nitrogen. Increases in the amount of available mineral nitrogen processed by rhizosphere organisms in the degraded prairie ecosystem results in increases in grass herbage biomass production and increases in plant density (basal cover) of the desirable native grass species. When the quantity of mineral nitrogen increases to 100 pounds per acre or greater, the defoliation resistance mechanisms can be fully activated that accelerate growth rates of replacement leaves and shoots, increase photosysnthetic capacity of remaining mature leaves, increase allocation of carbon and nitrogen, and increase secondary tiller development from axillary buds. The water use efficiency processes also are activated in grass plants resulting in an increase of 50.4% in herbage biomass production per inch of precipitation received. As restoration continues, native perennial grass species composition increases in the plant community. The native grasses out compete the less desirable and the undesirable species for space and nutrient resources because of the advantages provided by the symbiotic relationship with the rhizosphere organisms. The restoration of the native plant species composition lags behind the restoration of the prairie ecosystem biogeochemical processes and the recovery of the nitrogen cycle.

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