Restoration of Degraded Prairie Ecosystems

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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 grass plants, and the stimulation of these processes with defoliation by grazing animals.

Grass plants evolved 20 million years ago with early herbivores that are now extinct. During this time, grasses developed biological processes that help the plants withstand and recover from defoliation (Manske 2000a). This complex of processes (McNaughton 1979, 1983; Briske 1991; Briske and Richards 1995), called defoliation resistance mechanisms, accelerates both the growth rate of the grazed plant and its development of foliage and roots. Two biological processes of primary concern to grassland managers are the increased beneficial activity of soil organisms (Coleman et al. 1983) and the stimulation of vegetative reproduction by secondary tiller development from axillary buds (Briske and Richards 1995). Grazing that removes a small amount of leaf area from the grass plant between the third-leaf stage and flowering stage can trigger these beneficial responses (Manske 1999).

There is a mutually beneficial relationship between the grass plant's root system and soil organisms. The narrow zone of soil around the roots of perennial grassland plants, 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 plant's roots release carbon compounds (Campbell and Greaves 1990), including sugars, to these rhizosphere organisms, and the organisms release mineral nitrogen that the plant's roots 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 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 third-leaf stage and the flowering stage (Manske 1999) can increase the quantity of carbon compounds the defoliated plant releases into the rhizosphere (Hamilton III and Frank 2001). The increase in 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 seem to occur when grazing is conducted during the middle and late growth stages of the grass plant (Manske 2000a).

The primary cause of deterioration in prairie ecosystems is management practices that are antagonistic to the rhizosphere organism population. Decreases in rhizosphere organism biomass result in reductions in the quantity of organic nitrogen converted into inorganic nitrogen; this conversion is one of the primary functions of rhizosphere organisms. Decreases in the amount of inorganic nitrogen in an ecosystem cause reductions in grass biomass production and in native plant density (basal cover), creating larger and more numerous bare spaces between grass plants. These open spaces in the plant communities provide ideal habitat for growth of opportunistic "weedy" plant species that are not dependent on the nitrogen converted by rhizosphere organisms. The change in plant composition to greater abundance of plants that do not depend on rhizosphere organisms is basically a symptom, and the degree of plant species change lags behind the degree of ecosystem degradation.

Long-term non-defoliation (idle) management is a management choice that withholds defoliation from a grassland for a considerable length of time. Non-defoliation treatments increase the level of shading in a grassland ecosystem. Long-term nongrazed grass plants shift to erect growth forms with a small number of tillers with fewer leaves because the shading from other plants reduces the light intensity reaching the lower leaves of an individual plant (Briske and Richards 1995). Grass leaves grown under shaded

conditions become longer but narrower, thinner, and lower in weight (Langer 1972) than leaves in sunlight. Shaded leaves have a reduced rate of photosynthesis, which decreases the carbohydrate supply and causes a reduced growth rate of leaves and roots (Langer 1972). Root growth is reduced because roots are very sensitive to reductions in light intensity reaching the leaves. Shading also increases the rate of senescence in the lower, older leaves.

Decomposition of leaf material through microbial activity can take place only after the leaves have made contact with the soil. Standing dead material not in contact with the soil does not decompose but breaks down slowly as a result of leaching and weathering. Accumulation of standing dead leaves retains increasing portions of ecosystem nutrients aboveground and reduces availability of carbon and nitrogen in soil. Under nongrazed treatments, dead leaves remain standing for several years. Moreover, standing dead leaves shade early leaf growth in spring, slowing the rate of growth, reducing the leaf area, and causing a reduction in the net primary productivity. Long-term effects of shading in nongrazed grasslands include degraded total plant densities and native grass species composition (Manske 1995) and increased composition of shade-tolerant or shade-adapted replacement species like smooth bromegrass and Kentucky bluegrass. Increased mulch biomass resulting from long-term non-defoliation (Brand and Goetz 1986, Manske 1995) negatively affects the soil. Excessive mulch consisting mainly of broken off dead leaf and stem material reduces water infiltration and early season soil temperatures, causing reduced soil microbial activity in the top 12 inches of soil. Excess mulch accumulation also causes conditions that decrease mycorrhizal fungal and rhizosphere organism activity, slow nutrient cycles, decrease conversion of soil organic nitrogen into inorganic nitrogen, and reduce available nutrients including carbon and nitrogen.

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). Grazing that removes a small amount of young leaf tissue from the aboveground portion of lead tillers after the three-leaf stage and before the flowering stage reduces the amount of the inhibitory hormone in the plant (Briske and Richards 1994). With that inhibitory hormone reduced, the growth hormones stimulate vegetative reproduction (Murphy and Briske 1992, Briske and Richards 1994), and secondary tillers develop from the previous year's axillary buds (Langer 1972).

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 demands 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 third-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). Starting grazing after the third-leaf stage and before the flowering 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 flowering stage, as on a deferred grazing strategy, the lead tiller inhibits vegetative tiller development until the inhibitory hormone production naturally declines during the flowering 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 flowering 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 inorganic nitrogen. No evidence has been found to suggest that grazing the lead tiller after it has reached the flowering stage has beneficial stimulatory effects on vegetative tiller development or rhizosphere organism activity (Manske 2000a).

The twice-over rotation grazing management system applies defoliation treatment to grass plants at the appropriate phenological growth stages to stimulate the defoliation resistance mechanisms and the activity of the symbiotic rhizosphere microorganisms (Manske 1999, 2000a; Gorder, Manske, Stroh 2004).

The twice-over rotation grazing management system uses three to six pastures. Each of the pastures in the rotation 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 third-leaf and flowering 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 inorganic 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).

Biologically effective management practices that stimulate rhizosphere organism populations and enhance ecosystem biogeochemical cycles restore degraded prairie ecosystem processes; this restoration of nutrient cycling is followed by the improvement in plant composition to a greater abundance of species dependent on rhizosphere organisms.

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