PROGRESS REPORT
Defoliation Effects on the Structure and Dynamics of Grassland Ecosystems

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Abstract
Grassland plants developed defoliation resistance mechanisms to compensate for herbage removal by herbivores and fire during the long period of evolution. Two types of defoliation resistance mechanisms are of particular importance to grassland managers: changes in physiological responses within grassland plants and changes in activity levels of symbiotic soil organisms in the rhizosphere. Grassland managers can beneficially manipulate these defoliation resistance mechanisms by timing grazing for a short period (7-17 days) of partial defoliation of young leaf material between the third-leaf stage and anthesis phenophase. Grass tiller numbers, aboveground herbage biomass, and nutrient content of herbage increase as a result of plant defoliation at early phenological growth stages. These increases allow for subsequent increases in stocking rate and result in improved individual livestock weight performance during a second grazing period after anthesis.

Introduction
The diverse and complex nature of grassland ecosystems causes considerable difficulty in development of sound management recommendations. However, increasing knowledge of ecological principles and the intricacies of numerous mechanisms in the grassland ecosystem has allowed for development of improved management strategies.

Recently several greenhouse and laboratory studies have led to the initial understanding of defoliation resistance mechanisms grassland plants developed as evolutionary responses to defoliation by herbivores and fire. Defoliation resistance mechanisms are described in two
categories (Manske 1999). External mechanisms involve herbivore-induced environmental modifications (Briske and Richards 1995). Internal mechanisms are associated with herbivore-induced physiological processes (McNaughton 1979, McNaughton 1983) and are divided into two subcategories: tolerance mechanisms and avoidance mechanisms (Briske 1991). Defoliation tolerance mechanisms facilitate growth following grazing and include both increased activity within the plant meristem and compensatory physiological processes (Briske 1991). Defoliation avoidance mechanisms reduce the probability and severity of grazing and include the modification of anatomy and growth form. Grazing resistance in grass is maximized when the cost of resistance approximates the benefits. Plants do not become completely resistant to herbivores because the cost of resistance at some point exceeds the benefits provided by the resistance mechanisms (Pimentel 1988).

Grassland management by defoliation with herbivores has the greatest beneficial effect if planned to stimulate two mechanisms: vegetative tillering from axillary buds and increased activity of symbiotic soil organisms. The physiological responses to defoliation do not occur at all times, and the intensity of the response is variable. The physiological responses can be related to different phenological growth stages of the grass plants. The key to ecological management by effective defoliation is to apply defoliation during the phenological growth stage at which the desired outcome will be triggered.

Understanding the defoliation resistance mechanisms that work within grassland plants and that stimulate the symbiotic organisms in the rhizosphere following defoliation is necessary to accomplish beneficial manipulation of these mechanisms under field conditions and to develop ecologically sound recommendations for management of our grassland ecosystems. The goals of this research project were to study the ecological effects of defoliation and to determine the season of use for domesticated grasses and native range in the Northern Plains.

Methods and Materials

The long-term study site is on the Dickinson Research Extension Center ranch, operated by North Dakota State University and located 20 miles north of Dickinson in southwestern North Dakota, U.S.A. (47°14'N.lat., 102°50'W.long.).

Soils are primarily Typic Haploborolls. Mean annual temperature is 42.3°F (5.7°C). January is the coldest month, with a mean temperature of 14.0°F (-10.0°C). July and August are the warmest months, with mean temperatures of 68.9°F (20.5°C) and 68.9°F (20.5°C), respectively. Long-term annual precipitation is 16.31 inches (414.16 mm). The growing-season precipitation (April to October) is 13.81 inches (350.63 mm), 85.0% of annual precipitation (Manske 2002). The vegetation is the Wheatgrass-Needlegrass Type (Barker and Whitman 1988) of the mixed grass prairie. The dominant native range species are western wheatgrass (Agropyron smithii), needleandthread (Stipa comata), blue grama (Bouteloua gracilis), and threadleaved sedge (Carex filifolia).

The grazing treatments and nongrazed control were organized as a paired-plot design. The nongrazed control, 4.5-month twice-over rotation treatment, and 6.0-month seasonlong treatment had two replications. The 4.5-month seasonlong treatment had three replications. The long-term nongrazed treatments had not been grazed, mowed, or burned for more than 30 years prior to the start of data collection.
The 4.5-month twice-over rotation (4.5 TOR) management strategy began on a fertilized (50lbs N/acre on 1 April) crested wheatgrass pasture, with grazing starting as close as possible to 1 May and continuing on that forage type for about 31 days. The livestock then followed a rotation sequence through three native range pastures during the next 135 days. Each pasture was grazed for two periods, one period of 15 days between 1 June and 15 July (third-leaf stage to anthesis phenophase), followed by a second period of 30 days after 15 July and prior to mid October. The first pasture grazed in the sequence was the last pasture grazed the previous year. The livestock were moved to an Altai wildrye pasture on 15 October, where they grazed for about 30 days, until as close as possible to 15 November, when the calves were weaned at about 244 days of age.

The 4.5-month seasonlong (4.5 SL) management strategy began on an unfertilized crested wheatgrass pasture, with grazing starting as close as possible to 1 May and continuing on that forage type for about 31 days. The livestock were moved to one native range pasture on 1 June, where they grazed for 135 days, until 15 October. Cows and calves were then moved to crop aftermath, where they grazed for about 30 days, until as close as possible to 15 November, when the calves were weaned at about 244 days of age.

The 6.0-month seasonlong (6.0 SL) management strategy began as close as possible to 16 May, with grazing on one native range pasture. The livestock remained on this pasture for 183 days, until as close as possible to 15 November, when the calves were weaned at about 244 days of age.

Each treatment was stratified on the basis of three range sites (sandy, shallow, and silty sites). Samples from the grazed treatments were collected on both grazed quadrats and quadrats protected with cages (ungrazed). Aboveground plant biomass was collected on 11 sampling dates from April to November. The major components sampled were cool- and warm-season grasses, sedges, forbs, standing dead, and litter. Plant species composition was determined by the ten-pin-point frame method (Cook and Stubbendieck 1986) between mid July and August. A standard paired-plot t-test was used to analyze differences between means (Mosteller and Rourke 1973).

Commercial crossbred cattle were used on all grazing treatments in this trial. Individual animals were weighed on and off each treatment and on each rotation date. Cow and calf mean weights were determined for each grazing period. Live-weight performance of average daily gain and accumulated weight gain for cows and calves was used to evaluate each treatment. Cow animal unit equivalent (AUE) was determined through calculation of the metabolic weight of the average animal as a percentage of the metabolic weight of a 1000-pound cow (Manske 1998).

Results and Discussion

Forage feed costs of pasture-forage management strategies by range cow production periods are compared in table 1.

Forage feed for a range cow during the 32 days of the dry gestation production period, from mid November to mid December, cost $1.27 per day, or $40.64 per period, for native range pasture; $0.42 per day, or $13.44 per period, for mature crested wheatgrass hay; $0.44 per day, or $14.08 per period, for cropland aftermath pasture; and $0.38 per day, or $12.16 per period, for forage barley hay.
Forage feed for a range cow during the 90 days of the third trimester production period, from mid December to mid March, cost $1.67 per day, or $150.30 per period, for native range pasture; $0.62 per day, or $55.80 per period, for mature crested wheatgrass hay; and $0.38 per day, or $34.20 per period, for forage barley hay.

Forage feed for a range cow with a calf during the 45 days of the early lactation production period, from mid March to late April, cost $1.97 per day, or $88.65 per period, for native range pasture; $0.80 per day, or $36.00 per period, for crested wheatgrass-alfalfa-corn silage feed mix; and $0.41 per day, or $18.45 per period, for forage barley hay.

Forage feed for a range cow with a calf during the 31 days of the spring lactation production period, from early to late May, cost $1.35 per day, or $41.85 per period, for native range pasture; $0.52 per day, or $16.12 per period, for crested wheatgrass pasture; and $0.51 per day, or $15.81 per period, for fertilized crested wheatgrass pasture.

Forage feed for a range cow with a calf during the 137 days of the summer lactation production period, from early June to mid October, cost $1.16 per day, or $158.92 per period, for native range pasture managed by the 6.0-month seasonlong treatment; $0.81 per day, or $110.97 per period, for native range pasture managed by the 4.5-month seasonlong treatment; and $0.58 per day, or $79.46 per period, for native range pastures managed by the 4.5-month twice-over rotation management system.

Forage feed for a range cow with a calf during the 30 days of the fall lactation production period, from mid October to mid November, cost $1.59 per day, or $47.70 per period, during the early portion of the fall and $1.82 per day, or $54.60 per period, during the late portion of the fall for native range pasture grazed at the proper fall stocking rate; $1.18 per day, or $35.40 per period, for native range pasture grazed at the summer stocking rate (This high stocking rate during the fall is not sustainable.); $0.44 per day, or $13.20 per period, for cropland aftermath pasture; and $0.40 per day, or $12.00 per period, for Altai wildrye pasture.

The lowest cost forage feed for range cows is forage barley hay during the dry gestation period, the third trimester period, and the early lactation period; fertilized crested wheatgrass pasture during the spring lactation period; native range pastures managed by the twice-over rotation system during the summer lactation period; and Altai wildrye pasture during the fall lactation period.

The twice-over rotation system, used to manage native range during the 137 days of the summer lactation production period, applies defoliation treatments to grass plants at the appropriate phenological growth stages to stimulate the defoliation resistance mechanisms within the plants and the activity of the symbiotic microorganisms in the rhizosphere. This stimulation increases both secondary tiller development of grasses and nutrient flow in the rhizosphere, resulting in increased plant basal cover and aboveground herbage biomass and improved nutritional quality of forage. The increase in quantity and quality of herbage permits an increase in stocking rate levels, improves individual animal performance, increases total accumulated weight gain, reduces acreage required to carry a cow-calf pair for the season, improves net return per cow-calf pair, and improves net return per acre (Manske et al. 1988, Manske 1994, 1996).

After the defoliation resistance mechanisms have been stimulated by partial defoliation at the proper phenological growth stages, the quantity of herbage biomass produced is related to the amounts of sunlight and soil water available to the plants and by the amount of
remaining leaf surface area that is photosynthetically active. When cows remove a greater amount of leaf material than is required to promote high levels of herbage production, the quantity of standing herbage biomass is reduced.

**Conclusion**

Additional research is needed to quantify exudation material; soil organism activity and biomass; nitrogen, carbon, and phosphorus cyclic flows; and axillary bud development into tillers. Such research would lead to a more complete understanding of the defoliation resistance mechanisms of grassland plants and enable grassland managers to manipulate defoliation for the increased benefit of the grassland ecosystems.

Data have shown that defoliation of grass plants between the third-leaf stage and anthesis has beneficial effects on the physiological responses within the plant, which allow for greater tiller development, and beneficial effects on the symbiotic rhizosphere activity, which increase the amount of available nitrogen for plant growth. Deliberate and intelligent manipulation of these defoliation resistance mechanisms can increase secondary tiller development and total herbage biomass. The secondary tillers increase the nutrient content of the herbage and thereby improve individual animal weight performance during the later portion of the grazing season. The additional herbage biomass allows for a higher stocking rate and a greater amount of herbage remaining standing after grazing. Increased secondary tiller growth results in increases in plant density, canopy cover, and litter cover. These increases reduce the impact of raindrops, reduce and slow runoff, reduce erosion, and improve water infiltration.

The twice-over rotation strategy systematically grazes each of three to six native range pastures for two grazing periods. The first rotation period occurs between the third-leaf stage and anthesis phenophase (1 June to 15 July), with grazing for seven- to seventeen-days in each pasture, and the second rotation period occurs between mid July and mid October, with grazing in each pasture for a period double the length of the first. The combination of these two grazing periods maximizes the beneficial effects of the defoliation resistance mechanisms of grassland plants when adequate quantities of photosynthetically active leaf surface area remain standing after each grazing period.

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<th>Table 1. Pasture and forage costs for range cow production periods.</th>
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<td><strong>Dry Gestation 32 days mid Nov-mid Dec</strong></td>
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<td>Cost 1</td>
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<td>Cost 2</td>
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<td>Cost/day</td>
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<td><strong>Third Trimester 90 days mid Dec-mid Mar</strong></td>
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<td><strong>Early Lactation 45 days mid Mar-late Apr</strong></td>
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<td><strong>Spring Lactation 31 days early-late May</strong></td>
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<td><strong>Summer Lactation 137 days early Jun-mid Oct</strong></td>
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<td>Cost/day</td>
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<td><strong>Fall Lactation 30 days mid Oct-mid Nov</strong></td>
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<td>Pasture - Proper Stocking Rate</td>
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<td>Cost/day</td>
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