
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 the physiological responses within the grassland plants and changes in the activity levels of the symbiotic soil organisms in the rhizosphere. Grassland managers can beneficially manipulate these defoliation resistance mechanisms by timing grazing for a short period (7-15 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 defoliation at early phenological growth stages. These increases allow for subsequent increases in stocking rate and for improvement in 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. Increasing knowledge of ecological principles and the intricacies of the numerous mechanisms in the grassland ecosystem has allowed for development of improved management strategies.

Recently several greenhouse and laboratory studies have opened the way 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 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 stages of growth of the grass plants. The key to ecological management by effective defoliation is to apply defoliation during the phenological growth stage that triggers the desired outcome.

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 the season of use for domesticated grasses and native range in the Northern Great 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. ($47^{\circ}14'N$.lat., $102^{\circ}50'W$.long.).

Soils are primarily Typic Haploborolls. Mean annual temperature is 43.9EF (57EC). January is the coldest month, with a mean temperature of 13.4EF (-10.3EC). July and August are the warmest months, with mean temperatures of 73.0EF (20.4EC) and 72.6EF (20.3EC), respectively. Long-term annual precipitation is 15.99 inches (406.19 mm). The growing-season precipitation (April to October) is 13.59 inches (345.19 mm) and is 85.0% of annual precipitation (Manske 2000). 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, 4.5m twice-over rotation treatment, and 6.0m seasonlong treatment had two replications. The 4.5m 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 15 October and 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 1 June and grazed for 135 days, until 15 October. Cows and calves were then moved to crop aftermath and 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, sedge, 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. The statistical method used to analyze differences between means was a standard paired-plot t-test (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

The grazing period averaged 186, 190, and 183 days for the 4.5m twice-over rotation, 4.5m seasonlong, and 6.0m seasonlong treatments, respectively ([tables 1, 2, and 3](#)). The stocking rate averaged 2.10, 2.98, and 2.24 acres per animal unit month (AUM) for the 4.5m twice-over rotation, 4.5m seasonlong, and 6.0m seasonlong treatments, respectively (tables 4, 5, and 6), with each cow-calf pair evaluated as one animal unit without adjustment for animal weights differing from the standard animal unit of one 1000-pound cow with calf. The stocking rate averaged 1.67, 2.38, and 1.77 acres per animal unit equivalent month (AUEM) for the 4.5m twice-over rotation, 4.5m seasonlong, and 6.0m seasonlong treatments, respectively ([tables 4, 5, and 6](#)), when the average animal unit equivalent values were calculated for the animals on each treatment. These values represent about a 20% increase in stocking rate because of the increase in cow size.

Calf average daily gain (ADG) on 4.5m twice-over rotation, 4.5m seasonlong, and 6.0m seasonlong treatments was 2.54, 2.37, and 2.36 pounds, respectively ([table 7, 8, and 9](#)). Calf gain per acre (G/A) on 4.5m twice-over rotation, 4.5m seasonlong, and 6.0m seasonlong treatments was 36.9, 24.3, and 32.5 pounds, respectively ([table 7, 8, and 9](#)). Cow average daily gain (ADG) on 4.5m twice-over rotation, 4.5m seasonlong, and 6.0m seasonlong treatments was 0.53, 0.43, and 0.19 pounds, respectively (table 10, 11, and 12). Cow gain per

acre (G/A) on 4.5m twice-over rotation, 4.5m seasonlong, and 6.0m seasonlong treatments was 7.6, 4.4, and 2.8 pounds, respectively ([table 10, 11, and 12](#)). Calf and cow average daily gain and gain per acre were greater on the 4.5m twice-over rotation management strategy than on the 4.5m seasonlong and 6.0m seasonlong treatments.

The amount of live herbage that remained standing on the treatments after grazing ([table 13](#)) was less than the live herbage biomass on the long-term nongrazed control. This is a change from previously reported herbage data (Manske 1994) that showed the amount of live herbage remaining standing on 1 September after grazing on the twice-over rotation treatments was significantly greater than the amount of total current year's growth on the long-term nongrazed treatments. The difference between the two herbage amounts is accounted for by an increase in cow size in the current study. Cow body size affects the quantity of dry matter intake; large cows eat more forage than do cows of average size.

The twice-over rotation grazing management strategy 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 1996).

After the defoliation resistance mechanisms have been stimulated by partial defoliation at the proper phenological growth stages, the quantity of herbage biomass that results is affected by 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 larger 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 would enable grassland managers to manipulate defoliation for the increased benefit of the grassland ecosystems.

Data collected to date have shown that defoliation of grass plants between the third-leaf stage and anthesis phenological stage 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 increase in herbage biomass allows for an increase in stocking rate and a greater amount of herbage remaining

standing after grazing. As a result of increased secondary tiller growth, plant density, canopy cover, and litter cover increase. These increases reduce the impact of raindrops, reduce and slow runoff, reduce erosion, and increase water infiltration. Grazing management recommendations that systematically rotate 7- to 15- day periods of defoliation between the third-leaf stage and anthesis phenophase (1 June to 15 July in western North Dakota) on each pasture should maximize 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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Table 1. Grazing dates for 4.5m Twice-over Rotation treatments (mean 2 reps), 1998 and 1999.				
4.5 TOR	Treatments			
	Crested Wheat	Native Range	Altai Wildrye	System
1998				
Dates	5 May-2 Jun	2 Jun-7 Oct	7 Oct-4 Nov	5 May-4 Nov
# Days	28	127	28	183
# Months	0.92	4.16	0.92	6.0
Acres	28	235	30	293
# Cow-calf prs.	23	23	23	23
1999				
Dates	5 May-2 Jun	2 Jun-7 Oct	7 Oct-9 Nov	5 May-9 Nov

# Days	28	127	33	188
# Months	0.92	4.16	1.08	6.16
Acres	28	235	30	293
# Cow-calf prs.	23	23	23	23

Table 2. Grazing dates for 4.5m Seasonlong treatments (mean 3 reps), 1998 and 1999.				
4.5 SL	Treatments			
	Crested Wheat	Native Range	Crop Aftermath	System
1998				
Dates	5 May-2 Jun	2 Jun-15 Oct	15 Oct-12 Nov	5 May-12 Nov
# Days	28	135	28	191
# Months	0.92	4.43	0.92	6.26
Acres	15	80	53	148
# Cow-calf prs.	8	8	8	8
1999				

Dates	5 May-2 Jun	2 Jun-14 Oct	14 Oct-9 Nov	5 May-9 Nov
# Days	28	134	26	188
# Months	0.92	4.39	0.85	6.16
Acres	15	80	53	148
# Cow-calf prs.	8	8	8	8

Table 3. Grazing dates for 6.0m Seasonlong treatments (mean 2 reps), 1998 and 1999.		
6.0 SL	Treatments	
	Native Range	System
1998		
Dates	12 May-12 Nov	12 May-12 Nov
# Days	184	184
# Months	6.0	6.0
Acres	80	80
# Cow-calf prs.	6	6

1999		
Dates	12 May-9 Nov	12 May-9 Nov
# Days	181	181
# Months	5.9	5.9
Acres	80	80
# Cow-calf prs.	6	6

Table 4. Stocking rate pressure for 4.5m Twice-over Rotation treatments (mean 2 reps), 1998 and 1999.

4.5 TOR	Treatments			
	Crested Wheat	Native Range	Altai Wildrye	System
1998				
ac/hd	1.22	10.22	1.30	12.74
ac/AUM	1.32	2.46	1.42	2.12
AUE	1.23	1.27	1.27	1.26
ac/AUEM	1.08	1.93	1.12	1.69
ac/AUE	0.99	8.05	1.03	10.11

1999				
ac/hd	1.22	10.22	1.30	12.74
ac/AUM	1.32	2.46	1.21	2.07
AUE	1.23	1.28	1.23	1.26
ac/AUEM	1.08	1.93	0.98	1.64
ac/AUE	0.99	7.98	1.06	10.11

Table 5. Stocking rate pressure for 4.5m Seasonlong treatments (mean 3 reps), 1998 and 1999.

4.5 SL	Treatments			
	Crested Wheat	Native Range	Crop Aftermath	System
1998				
ac/hd	1.89	10.00	6.63	18.50
ac/AUM	2.04	2.26	7.20	2.96
AUE	1.23	1.26	1.25	1.25
ac/AUEM	1.66	1.79	5.76	2.36

ac/AUE	1.52	7.94	5.30	14.80
1999				
ac/hd	1.89	10.00	6.63	18.50
ac/AUM	2.04	2.28	7.79	3.00
AUE	1.23	1.26	1.24	1.25
ac/AUEM	1.66	1.81	6.29	2.40
ac/AUE	1.52	7.94	5.34	14.80

Table 6. Stocking rate pressure for 6.0m Seasonlong treatments (mean 2 reps), 1998 and 1999.

6.0 SL	Treatments	
	Native Range	System
1998		
ac/hd	13.33	13.33
ac/AUM	2.22	2.22
AUE	1.27	1.27

ac/AUEM	1.75	1.75
ac/AUE	10.50	10.50
1999		
ac/hd	13.33	13.33
ac/AUM	2.26	2.26
AUE	1.27	1.27
ac/AUEM	1.78	1.78
ac/AUE	10.50	10.50

Table 7. Calf performance on 4.5m Twice-over Rotation treatments (mean 2 reps), mean 1998 and 1999.				
4.5 TOR	Treatments			
	Crested Wheat	Native Range	Altai Wildrye	System
1998-1999				
Calf ADG	2.56	2.73	1.69	2.54
G/A	58.9	33.9	39.6	36.9

Table 8. Calf performance on 4.5m Seasonlong treatments (mean 3 reps), mean 1998 and 1999.

4.5 SL	Treatments			
	Crested Wheat	Native Range	Crop Aftermath	System
1998-1999				
Calf ADG	2.46	2.57	1.29	2.37
G/A	36.7	34.6	5.1	24.3

Table 9. Calf performance on 6.0m Seasonlong treatments (mean 2 reps), mean 1998 and 1999.

6.0 SL	Treatments	
	Native Range	System
1998-1999		
Calf ADG	2.36	2.36
G/A	32.5	32.5

Table 10. Cow performance on 4.5m Twice-over Rotation treatments (mean 2 reps), mean 1998 and 1999.

4.5 TOR	Treatments			
	Crested Wheat	Native Range	Altai Wildrye	System
1998-1999				
Cow ADG	2.44	0.28	-0.15	0.53
G/A	56.0	3.5	-4.7	7.6

Table 11. Cow performance on 4.5m Seasonlong treatments (mean 3 reps), mean 1998 and 1999.

4.5 SL	Treatments			
	Crested Wheat	Native Range	Crop Aftermath	System
1998-1999				
Cow ADG	1.09	0.55	-0.81	0.43
G/A	16.2	7.3	-3.3	4.4

Table 12. Cow performance on 6.0m Seasonlong treatments (mean 2 reps), mean 1998 and 1999.

6.0 SL	Treatments	
	Native Range	System
1998-1999		
Cow ADG	0.19	0.19
G/A	2.8	2.8

Table 13. Standing live herbage biomass (lbs/ac) remaining after grazing by sample periods for 3 grazing treatments and nongrazed control (mean 2 reps), mean 1998 and 1999.

	SAMPLE PERIODS										
	15 Apr	1 May	15 May	1 Jun	15 Jun	1 Jul	15 Jul	15 Aug	15 Sep	15 Oct	15 Nov
Nongrazed Native Range				1106	1666		2240	1856	1901	1649	
6.0 SL Native Range			783	969	1345		1435	1225	1082	825	829
4.5 SL Crested Wheat	762	1197		1088	1492		1839	1632	1441	1447	

Native Range				1099	1480		1641	1458	1299	1008	
4.5 TOR Crested Wheat	986	1589		1319	1914		2851	2402	1969	2042	
Native Range				970	1281	1458	1368	1327	991	868	
Altai Wildrye	863	1229		1833			3092	2887	3235	3294	995

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