



Grasslands of the Missouri Coteau and their relationship to environment
by John Bernard Plaggemeyer

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of
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Montana State University
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Abstract:

Short, mixed, and tallgrass prairie of the great plains are contrasted where they appear together in the pothole topography of the northern plains. Chapters of this document answer six major questions. 1) Environments of the prairie types are contrasted with respect to environment (water availability is the principle control) and responses in composition, diversity, and process (including productivity). 2) Fuel loads affect fire probability and performance. Quantities of litter and standing material are contrasted across Coteau grasslands and via literature review, grasslands of the entire great plains. 3) After fire, the litter component accumulates for 3-5 years and contributes to both fuel load and differentiation of microenvironments with respect to ground level light, temperature, moisture, and nutrient availability. 4) Because quantities of standing crop contribute to management issues including animal cover, fire management, exotic invasion, the manager needs periodic inventory of standing biomass and litter over wide areas. We compared reflectance in Landsat wavebands of sites with various fitter and standing crop loads, ie reflectance in spring and summer and reflectance on short, mixed, and tall grass prairie. We found that reflectance alone was a poor predictor of fuel ($r^2=0.262$), that prediction improved if supplemental data (topography) was included ($r^2=0.560$), and that prediction was improved still further if information from several dates was included ($r^2=0.725$). 5) Arrival of white man has modified vegetation of the mixed grass prairie, our median environment, by excluding fire and introducing exotics. To evaluate the effects we compared mixed grass ecosystems with systems occupying identical environments but dominated by snowberry or brome grass. Productivities were 268g/m² on bottom sites, 207g/m² on mid slopes, and 141g/m² on ridgetops. 6) Since further exotic invasion may be expected, we asked which environments (dry of shortgrass to moist of tallgrass) and, in the mixed grass prairie, which community types are most easily invaded.

We tested this by observing the success of surrogate weeds (a grass and a forb) planted into our five community types. Our phytometers showed no significant difference in invariability.

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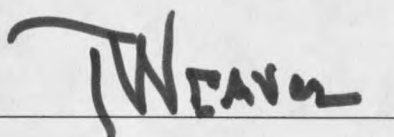
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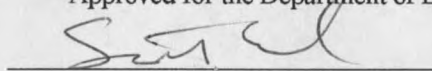
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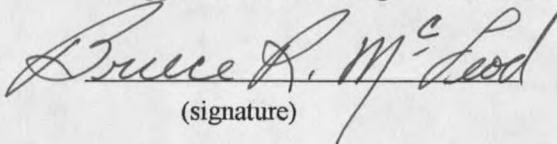
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ABSTRACT

Short, mixed, and tallgrass prairie of the great plains are contrasted where they appear together in the pothole topography of the northern plains. Chapters of this document answer six major questions. 1) Environments of the prairie types are contrasted with respect to environment (water availability is the principle control) and responses in composition, diversity, and process (including productivity). 2) Fuel loads affect fire probability and performance. Quantities of litter and standing material are contrasted across Coteau grasslands and via literature review, grasslands of the entire great plains. 3) After fire, the litter component accumulates for 3-5 years and contributes to both fuel load and differentiation of microenvironments with respect to ground level light, temperature, moisture, and nutrient availability. 4) Because quantities of standing crop contribute to management issues including animal cover, fire management, exotic invasion, the manager needs periodic inventory of standing biomass and litter over wide areas. We compared reflectance in Landsat wavebands of sites with various litter and standing crop loads, ie reflectance in spring and summer and reflectance on short, mixed, and tall grass prairie. We found that reflectance alone was a poor predictor of fuel ($r^2=0.262$), that prediction improved if supplemental data (topography) was included ($r^2=0.560$), and that prediction was improved still further if information from several dates was included ($r^2=0.725$). 5) Arrival of white man has modified vegetation of the mixed grass prairie, our median environment, by excluding fire and introducing exotics. To evaluate the effects we compared mixed grass ecosystems with systems occupying identical environments but dominated by snowberry or brome grass. Productivities were 268g/m^2 on bottom sites, 207g/m^2 on mid slopes, and 141g/m^2 on ridgetops. 6) Since further exotic invasion may be expected, we asked which environments (dry of shortgrass to moist of tallgrass) and, in the mixed grass prairie, which community types are most easily invaded. We tested this by observing the success of surrogate weeds (a grass and a forb) planted into our five community types. Our phytometers showed no significant difference in invadability.

CHAPTER 1

INTRODUCTION

The Central American prairies consist of different types of grasslands. Types of prairie are largely determined by the amount of rainfall and the substrate upon which that vegetation develops (Axelrod 1985; Bazzaz & Parrish 1982; Bragg & Steuter 1996; Risser 1985). Each prairie is characterized by a distinctive taxa (Bazzaz & Parrish 1982). Generally the most easterly plains receives more precipitation than the most westerly plains (Axelrod 1985; Risser 1985) and is referred to as the tall grass prairie or true prairie. The most westerly portion is the driest prairie and is referred to as the shortgrass prairie. The portion between these two prairies is called the mixed grass prairie and is intermediate in rainfall and is characterized by species from both the tall grass and short grass prairie (Bragg & Steuter 1996).

Lostwood National Wildlife Refuge (NWR) is located on the Missouri Cotcau which is the terminal moraine of glaciers that advanced and retreated many times over the northern Great Plains pushing soil and rocks leaving mixed material of rocks, soil, and chunks of ice during recent ice ages (Pielou 1991; Kruse & Bowen 1996; U.S. Fish and Wildlife Service 1998). As the glaciers melted at the end of the last ice age the resulting topography consists of many undrained basins.

Dry sites or ridgetops on Lostwood NWR have vegetation typical of the short grass type (Weaver 1968; Bragg and Steuter 1996; Sims & Risser 2000). Moist sites (bottom of coulees and next to the pothole pond) have plants typically found in the tall grass prairie. Intermediate sites between the ridges and the pond have species from the other two types with additional species present only on the slopes. This relationship allows us to study vegetation types which model short, mixed, and tallgrass prairies in essentially the same climate. We studied micro-environmental effects on the vegetation by studying soil characteristics, soil temperature differences, and water availability differences between sites. These effects on the vegetation were quantified by measuring biomass components using on the ground measurements (eg. clipping) and remotely by using a handheld radiometer. Biomass components that we considered were litter, spring standing crop, end-of-season standing crop, and combinations of these components (spring fuels and end-of-season fuels) that are of importance to land managers.

The various chapters in this dissertation deal with individual elements of these topics. Chapter 2 reports on the general microclimate and biomass components on the Contcau. Chapter 3 studies fuel loads on the three vegetation types that maybe useful to managers involved in fire management. Chapter 4 looks at litter effects on these prairies. Chapter 5 is concerned with the conversion of mixed grass prairies to exotic plants such as Smooth Brome or conversion to a type dominated by shrubs such as Western Snowberry. Chapter 6 reports on the invadability of these prairies using phytometers as a tool. The last chapter (Chapter 7) investigates the usefulness of a hand held radiometer to measure biomass components in various seasons. The methods may be convertible to satellite imagery use.

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CHAPTER 2

NORTHERN PRAIRIE

ENVIRONMENT AND VEGETATION TYPES

Introduction

The glaciated (northern) half of North Dakota has a rolling landscape with many pothole ponds (Pielou 1991, 1998). The resulting rolling topography is due to underlying bedrock and an overlying till which is thickest in the terminal moraine (Missouri Cotcau) just north of the Missouri River. Occasional lakes fill basins generated by morainal ridges and numerous 'pothole ponds' fill holes left by the melting ice blocks once embedded in the moraine.

Vegetation of the pothole basins varies with types that model tallgrass, mid-grass, and shortgrass prairie vegetation types. Vegetation near the pond edges is similar to tall grass prairie vegetation type (Weaver & Fitzpatrick 1934; Weaver 1968; Bragg and Steuter 1996; Sims & Risser 2000) and includes *Andropogon gerardi* and *Spartina pectinata*. Aspen (*Populus tremuloides*) may occupy these moist sites. A type similar to mixed grass (Weaver & Fitzpatrick 1934; Weaver 1968; Sims & Risser 2000) occupies slopes above the pondside vegetation which includes grass species such as *Schizachyrium scoparium*, *Poa pratensis*, and *Agropyron smithii* and shrubs, especially *Symphoricarpus occidentalis*. Higher dry ridge sites support shortgrass vegetation (Weaver 1968; Bragg and Steuter 1996; Sims & Risser 2000) with grass species such as *Stipa comata*, *Bouteloua gracilis*, and *Koeleria micrantha*.

The juxtaposition of tall, mixed, and shortgrass prairies in nearly identical soil and climate offers the possibility to compare major ecosystems of the Great Plains (Weaver & Rowland 1952; Dix 1960; Hulbert 1969, 1988; Hobbs et al. 1991). We compared grassland vegetation with respect to composition, function (phenology and production), and environment (soil temperature, soil water, and nutrients) to test the hypothesis that water availability caused by drainage from highlands toward lowlands is the primary factor in determining where we find vegetation types similar to tall grass, mixed grass, and shortgrass prairies.

Methods

Study Sites

Our study was conducted on the Lostwood National Wildlife Refuge, Kenmare, North Dakota in the mixed grass prairie zone of the northern plains (Kuchler 1964). The refuge lies on the Missouri Coteau, the terminal moraine of the continental glacier (Pielou 1991, 1998). Lostwood NWR has a landscape typical of pothole terrain with rolling topography including potholes with adjacent low (tall-grass), slope (mixed grass), and hilltop (short grass) grasslands. The continental climate of Lostwood NWR has cold winters and hot summers. Its temperatures are comparable to those across the northern plains (Coupland 1961; Weaver 1980); average min/max are (-10C) in January and 21C in July. Average annual rainfall for 1936 to 1989 was 419mm(309mm-497mm) (Kruse & Bowen 1996). Much of the rainfall in the western Great Plains falls in the May-June period (Weaver 1980). Great Plains zonal vegetation is determined by the water gradient extending from the moister eastern plains to the drier western plains (Weaver 1938, 1968; Risser et al 1981; Walter 1984; Axelrod 1985; Collins 1987; Anderson 1990; Collins & Gibson 1990; Simms & Risser 2000). Lostwood's precipitation (419 mm, Kruse & Bowen 1996) is intermediate between that of tallgrass prairie to the east (1000mm, Simms & Risser 2000) and shortgrass prairie to the west (300 mm, Simms & Risser 2000). Its normal drought lengths are intermediate between those of tallgrass and shortgrass prairie (Weaver 1980). Drought length may be most important in distinguishing grasslands and grasslands from other vegetation types (Risser et al 1981; Axelrod 1985). Great Plains zonal soils are mollisols ranging from Udolls and Aquolls under tallgrass prairies through Borolls under mixed grass to Ustolls and Xerolls under shortgrass prairies (Bragg 1995)

Community Sanding Crop

We compared standing crops on eleven representative transects to examine the effect of three topographic levels and the effect of time since fire. Burning time was replicated when possible. Our sites received zero to light grazing during the ten years (1989-1999) before our measurements and no grazing during the measurement period.

To estimate grazing effects we added simulated grazing treatments at each of the thirty-three sites described above. At each site we staked three 3x4m plots side-by-side on the contour with a one meter buffer between the plots. After staking, three treatments were randomly assigned to the plots. The first treatment was unclipped (untreated). In the second, standing dead was removed in the spring by mowing to 3 cm with a 'weed whip' and raking it off without disturbing the litter. In the third, standing dead was cut and both it and litter were vigorously raked. These levels approximate 'no grazing', 'moderate grazing' which removes most standing crop and 'heavy grazing' which removes both standing crop and litter (Aldous 1930; Penfound 1964; Hulbert 1988).

The weight of each standing crop component was estimated as follows. Current production in the un-grazed, moderately grazed, and heavily grazed plots at each of the thirty-three sites was sampled in all 3x4m plots with an August harvest (1998, 1999, and 2000) of material in two 1x2 (30x60 cm) foot plots; forage was clipped, dried, weighed, and data were scaled up to g/m^2 . Spring standing crop was estimated in 1999 by cutting all forage in the moderately grazed plot to 3 cm with a weed whip, collecting it with a broom rake, weighing it wet, and using the dry wt/wet weight of a 10% sample to adjust wet weight to dry weight. Litter was estimated in spring 1999 by cutting and measuring standing crop (as above) then vigorously raking the 3x4m plot to collect all litter. Litter dry weight was estimated by weighing the litter wet, sampling (10%), and then multiplying wet weight by the dry weight/ wet weight ratio of the sample to find the dry weight. Because vigorous raking also captured soil, the dry weight was further corrected by subsampling (33% of the 10%), ashing, and multiplying estimated dry weight by (sample weight -ash weight)/ sample weight.

Reflectance was measured periodically at each of the 99 sub-sites (11 units x 3 topographic positions x 3 grazing treatments) throughout the seasons of 1998, 1999, and 2000 as an index of phenology and production. 1) Eight, eight, and two dates were sampled respectively in 1998 (April 17-24, May 18-25, June 10-13, June 23-27, July 9-12, July 27-30, August 20-26, & September 12-15), 1999 (April 23-26, May 9-12, May 26-29, June 12-17, July 7-13, July 30-August 3, August 22-27, & Oct 30-Nov 3), and 2000 (May 3-7 & June 3-7). 2) Measurements were made with a 'Cropscan differential radiometer' which compares incoming radiation with reflected radiation in the blue (485 nm), green (560 nm), red (660 nm), near infrared

(830 nm) and infrared (1650 nm) bands (Aase et al. 1987; Goodin & Henebry 1997). We calculated NDVI (normalized difference vegetation index, $(\text{NIR}-\text{Red})/(\text{NIR}+\text{Red})$) (Wessman et al 1997; Davidson & Csillag 2001) and used it as an index of phenology and biomass. 3) The usual precautions were taken to avoid biasing reflectance data. To minimize sun angle effects, measurements were made at mid-morning (9:00-11:00am) and mid-afternoon (1:30-5:00pm) only (Goodin & Henebry 1997). Measurements were not made on excessively cloudy days. Time of measurement was rotated among plots to remove variation associated with the time of measurement. We tested the effect of time of day on reflectance against time of day by plotting time of day against each color band (Neter et al. 1990). We saw no time of day trend in the plots.

Plant species nomenclature follows the Great Plains Flora Association (1991).

Environmental Qualities

Environmental changes on the topographic and vegetation gradients hypothesized from vegetation differences were verified with field sampling. 1) Soil water was measured periodically over three years using plaster blocks buried at 15cm (Gardner 1986). Conductivity measured with an ohm-meter was calibrated against soils with known water contents (Campbell & Gee 1986). 2) Soil temperature was measured simultaneously with thermocouples buried at 15cm and a micro-volt meter (Taylor & Jackson 1986).

To compare evaporation among sites, we placed evaporimeters at bottom, slope and top sites on eight slope transects. Evaporimeter design was our own, but inspired by Piche (1872). The evaporimeter consisted of an evaporative surface, a water supply above it, and a supporting pole (steel fence post). The evaporative surface was a filter paper disc (10cm dia., Whatman #4 qualitative). Water was gravity fed to the plate from the inverted bottle (1Liter) through a 15cm plastic tube glued to the top of the bottle and an inverted funnel (2.5cm) standing on the evaporative surface. Evaporation rate was measured by adding a measured amount of water to the plastic bottle, allowing evaporation for 48 hours and re-measuring remaining water. We standardized our observations to 24 hours for our data point.

Snow measurements were taken in mid-March 1999 at each topographic position on the eleven sites and the depth of water in the snow at each location was calculated.

Soil Characteristics

The MSU soil testing lab measured carbon, nitrogen, pH, and conductivity (salinity) of soil samples from each site as indicators of soil nutrients/toxicity. Carbon and nitrogen were measured with the LECO CNS (Nelson & Summers 1996; Bremner 1996). Conductivity and pH were measured on 1:1 soil water slurries with appropriate meters (Thomas & Rhoades 1996). Soil texture was measured with the Boyoucos hydrometer method (Gee & Bauder 1986).

Statistical Analysis

Systat (SPSS, Inc 2000) was used to make our statistical analysis which included multiple regressions and ANOVA in our analysis.

Results

Environmental Contrasts

Experimental Design. The design of our study and major results are outlined in Table 2.1. Ridge, slope, and bottom (shortgrass, mixed, and tallgrass) ecosystems are compared on eleven transects ranging from recently burned (<2 years) to long unburned (>50 years). Column 1 lists 11 transects. Column 2 dates the last fire; time since fire can be calculated by subtracting 'burn date' from the current date. The body of the table compares standing crop and soil characteristics of these treatments.

Soil Water. Soils remained wet in all locations and positions on the hill from late April (our earliest measurement period) until July (Table 2.2). This is the period on the Great Plains during which a large proportion of the annual precipitation occurs (Coupland 1950, 1961). Plots with different burning histories were not significantly different in water availability ($p=0.05$ level). In July the ridgetops became dryer than the mid slope or bottom soils ($p=0.05$ level). During August the ridgetops and mid slopes dried more than the bottom soils next to the pond. Ridgetops were also dryer than mid slopes. These water values suggests that soil is dryer than the wilting point in the top 15cm for two week periods during late July and August (Fitter & Hay 1987).

Table 2.1. Sample sites studied, their fire histories, vegetation types, biomass components and soil characteristics.

Site	Year Last burned	SC spr ¹ 1999	litter spr ² 1999	SC ³ EOS (98-00)	Soil Org.	Soil PH	Soil EC	Soil C(%)	Soil N(%)	Soil C/N Ratio
<i>Hill top-Short Grass</i>										
Tower	1997	58	55	114	7.33	7.1	618	4.24	0.387	11.0
Iverson	1997	47	62	187	5.71	7.3	376	2.97	0.261	11.4
Aspen	1996	23	52	123	7.75	6.3	556	4.27	0.383	11.1
SC Core	1995	86	271	180	6.80	6.8	343	4.20	0.371	11.3
HQ-Sth	1995	128	178	140	8.41	6.3	634	4.75	0.392	12.1
NCCore	1995	39	51	136	6.60	7.6	485	4.53	0.372	12.2
Field 7	1994	35	138	104	5.67	7.6	450	3.44	0.288	11.9
T. Lake	1992	72	247	168	7.60	6.3	341	4.51	0.413	10.9
'87 Burn	1987	85	330	172	7.55	7.5	664	4.40	0.351	12.5
Wilder.	>50 ⁴	52	420	137	5.17	6.9	646	4.69	0.443	10.6
HQ-Nth	>50 ⁴	31	66	131	7.75	7.7	479	3.99	0.302	13.2
<i>Mid slope-Mixed Grass</i>										
Tower	1997	75	63	220	10.72	7.2	444	6.06	0.524	11.6
Iverson	1997	113	668	190	9.15	6.5	230	3.98	0.317	12.6
Aspen	1996	105	71	218	11.18	6.7	534	6.07	0.521	11.7
SC Core	1995	105	131	139	7.12	7.5	489	4.59	0.401	11.4
HQ-Sth	1995	153	558	272	11.85	6.1	317	7.04	0.573	12.3
NC Core	1995	156	410	224	10.68	6.7	476	5.72	0.480	11.9
Field 7	1994	65	389	149	7.70	7.4	440	4.19	0.356	11.8
T. Lake	1992	98	207	221	9.81	6.4	235	4.56	0.398	11.5
'87 Burn	1987	97	247	142	8.87	6.8	545	5.11	0.445	11.5
Wilder.	>50	22	326	214	7.93	7.2	422	2.81	0.246	11.4
HQ-Nth	>50	153	598	198	4.86	6.5	386	4.58	0.371	12.3
<i>Bottom-Tall Grass</i>										
Tower	1997	235	183	320	14.37	5.0	750	9.28	0.772	12.0
Iverson	1997	35	3	181	12.05	6.3	414	5.97	0.475	12.6
Aspen	1996	114	166	217	12.9	8.0	650	8.43	0.718	11.7
SC Core	1995	38	120	219	13.27	7.3	583	7.16	0.596	12.0
HQ-Sth	1995	132	661	341	15.63	5.7	348	8.91	0.745	12.0
NC Core	1995	133	261	273	11.1	5.6	245	6.38	0.524	12.2
Field 7	1994	199	827	353	13.1	7.7	489	6.99	0.634	11.0
T. Lake	1992	75	142	234	4.62	7.7	430	3.19	0.210	15.2
'87 Burn	1987	89	290	316	14.37	6.1	351	7.81	0.629	12.4
Wilder.	>50	121	679	311	12.57	8.2	279	2.93	0.173	17.0
HQ-Nth	>50	66	381	154	3.98	5.8	486	5.73	0.469	12.2

1. Standing crop vegetation measured early in the spring before greenup.

2. Biomass that has fallen to the soil surface measured early in the spring before greenup.

3. Biomass that was produced by the plants during the current year (three years average) measured in late August of each year

4. For sites with known burning history the actual year that it was burned is given. Sites that have not been burned in known time were assigned >50 years. To calculate time since burn subtract year last burned from the year of interest.

We investigated the physical processes that may be creating these soil moisture differences. 1) Rainfall amounts should not vary between topographic positions on the hill because the sites are close together (less than 500m). 2) Snow accumulation differed among topographic positions (Table 2.3). There was less average snow water on the ridgetops than on the slopes or in the bottoms ($p < 0.001$). We found a significant difference between snow accumulation of sites with different fire histories. However, there was a significant interaction between topographic location and fire history. Bottoms received more snow water on recently burned sites; ridgetop sites received more snow water on the sites that had not been burned for longer periods of time (Table 2.4). 3) We speculated that ridgetops may have higher evaporation rates. Even though ridgetops are most likely windier than depressions, we found no significant differences in evaporation rates between the different topographic positions (Table 2.3, $p = 0.854$). 4) Soil differences may affect water availability. Similarity of soil textures on the topographic gradient suggest that drainage will be similar on all position; however, drainage may be countered by capillary rise in bottoms.

Soil Temperatures

Soils at 15 cm warmed from April (bottoms= 5.7°C , slopes 6.7°C , and tops= 6.9°C) until late July (bottoms= 17.0°C , slopes 17.9°C , and tops= 18.9°C). We found significant differences between topographic levels throughout this period. Bottom plots were always colder than ridgetops (Table 2.4). Mid-slopes and ridgetops had similar soil temperatures from April until early June. In June mid-slopes sites became more like ridgetops. During July and August all three topographic levels were significantly different from each other (Table 2.4, $p = 0.001$). Bottom sites were cooler than slopes which were cooler than ridgetops in July and August.

Bottom sites were not affected by fire history at any time during the growing season. At mid-slope sites that had been burned recently (1-5 years) were warmer than sites that had not been burned for 5 to 50 years throughout the growing season ($p = 0.05$ level). On the ridgetops we found similar differences on mid-slopes between the recently and long unburned sites; however, after May burning history did not affect soil temperatures on ridgetop sites (Table 2.4).

Table 2.2. Water conditions on northern prairie by geographic position and years since the site was last burned.

		Bottom	Mid Slope	Top	Topo p-value
Soil Water ¹					
April					
	Mean	-0.00±0.01 B	-0.01 ±0.01A	-0.02 ±0.01A	<0.001, F=20.0, 87df
	1-3 years	-0.01a	-0.01a	-0.02a	
	4-5 years	-0.00a	-0.00a	-0.00a	
	5-10 years	-0.00a	-0.01a	-0.05a	
	10-50 years	-0.00a	-0.02a	-0.02a	
	fire p value	0.35,1.14,26df	0.02,3.98,26df	0.004,5.63,26df	
May					
	Mean	-0.00 ±0.04A	-0.01 ±0.04A	-0.19 ±0.04A	0.06, F=1.95, 288df
	1-3 years	-0.00a	-0.01a	-0.50a	
	4-5 years	-0.00a	-0.01a	-0.01a	
	5-10 years	-0.00a	-0.01a	-0.02a	
	10-50 years	-0.01a	-0.01a	-0.22a	
	fire p value	0.32,1.17,92df	0.48,0.84,95df	0.31,1.21,92df	
June					
	Mean	-0.30 ±0.20A	-0.67 ±0.20A	-0.99 ±0.20A	0.09, F=5.76, 258df
	1-3 years	-0.66a	-1.08a	-1.53a	
	4-5 years	-0.00a	-0.08a	-0.04a	
	5-10 years	-0.00a	-0.83a	-1.44a	
	10-50 years	-0.00a	-0.28a	-0.97a	
	fire p value	0.09,2.27,83df	0.11,2.06,84df	0.20,1.59,83df	
July					
	Mean	-1.20 ±0.30A	-3.46 ±0.25B	-2.90 ±0.30B	<0.001, F=15.5, 282df
	1-3 years	-0.82a	-3.53a	-3.03a	
	4-5 years	-1.39a	-2.02a	-1.67a	
	5-10 years	-0.08a	-4.04a	-3.37a	
	10-50 years	-2.06a	-3.63a	-3.52a	
	fire p value	0.05,2.71,80df	0.20,1.52,80df	0.43,0.92,80df	
August					
	Mean	-1.91 ±0.23 A	-3.58 ±0.19B	-4.56 ±0.24C	<0.001, F=27.9, 393df
	1-3 years	-1.68a	-4.14b	-4.24a	
	4-5 years	-2.05a	-4.62b	-5.65a	
	5-10 years	-0.43a	-4.10b	-4.57a	
	10-50 years	-2.95b	-2.04a	-3.81a	
	fire p value	0.01,4.15,110df	0.01,7.16,110df	0.07,2.37,110df	

1. Soil water is measured in megapascals at 15cm soil depth with significance to p=0.05 level.

Our treatments (removing standing crop and litter) did not affect soil temperatures in our plots in April ($p=0.159$), May ($p=0.452$), June ($p=0.169$), or July ($p=0.207$). Our treatment of clipping and/or raking the plots did affect soil temperature in August ($p=0.04$). Litter/standing crop free and standing crop free plots averaged 17.2°C and 17.1°C in August. The control plots (16.7°C) were significantly cooler than the treated plots during August.

Table 2.3. Processes contributing to differences in summer water availability.

	Bottom	Mid Slope	Top	Topo p value ¹
Evaporation ²	36.9 $\pm$ 6.1A	33.3 $\pm$ 6.1A	38 $\pm$ 6.1A	0.85, F=0.08, 17df
Snow Water ³				
Mean	8.3 $\pm$ 0.63B	7.4 $\pm$ 0.63B	3.4 $\pm$ 0.63A	0.001, F=16.3, 105df
1-3 years	11.6b	11.7b	2.9a	
4-5 years	4.7a	4.7a	3.0a	
5-10 years	5.0a	5.0a	2.7a	
10-50 years	5.5a	5.5a	4.7b	
Fire p-value	0.01,3.72,30df	0.01,4.41,33df	0.02,4.09,30df	

1. Means with different letters are significant to $p=0.05$ level.

2. Evaporation is measured in milliliters ($\pm$ SE) of water evaporated from a #4 filter paper for 24 hours.

3. Snow water is measured in centimeters ($\pm$ SE) of water in each measurement of snow.

Soil Properties on the Topographic Gradient

Soils developing on glacial till are young (less than 10,000 years since glaciation) with little development of unique characteristics on a site (Coupland 1950,1961; Pielou 1991). There was little difference between the ridgetop, mid slope, and bottom soils. At Lostwood textures on all three topographic locations were sandy (Table 2.5). Inorganic chemical features of the soils were also similar between topographic locations (Table 2.5). All soils were neutral or slightly acidic. We did find some significant differences in organic components among topographic locations (Table 2.5). Total soil organic matter was higher next to the pond than on the ridgetop. This is likely a result of higher levels of production next to the pond (Table 2.7). Bottom soils had higher levels of carbon and nitrogen ($p=0.05$ level). Carbon/nitrogen ratios did not vary significantly with topographic locations (Table 2.5, $p=0.121$). Carbon and nitrogen enrichment in bottoms was a result of higher production in bottoms.

Table 2.4. Soil temperature of northern prairie by geographic position and years since the site was last burned.

		Bottom	Mid Slope	Top	p value
April ¹	Mean ²	5.7 ± 0.4A	6.7 ± 0.4B	6.9 ± 0.4B	0.03, F=3.5, 870df
	1-3 years	5.9a	7.8b	8.0b	
	4-5 years	6.3a	8.8b	9.7b	
	5-10 years	5.3a	4.4a	4.8a	
	10-50 years	5.2a	4.9a	5.2a	
	fire p value	0.59,0.66,26df	0.001,8.53,26df	0.001,21.15,26df	
May ¹	Mean ²	10.7 ± 0.2A	11.4 ± 0.2B	12.1 ± 0.2B	<0.001, F=9.87, 288df
	1-3 years	11.2a	12.1b	12.3a	
	4-5 years	10.2a	12.3b	12.5a	
	5-10 years	11.0a	11.1a	12.2a	
	10-50 years	10.2a	10.4a	11.4a	
	fire p value	0.13,1.95,92df	0.001,6.01,92df	0.30,1.21,92df	
June ¹	Mean ²	13.6 ± 0.2A	14.1 ± 0.2A	14.9 ± 0.2B	0.006, F=8.28, 258df
	1-3 years	13.9a	14.4b	15.1a	
	4-5 years	13.5a	15.3b	15.9a	
	5-10 years	14.1a	13.3a	14.3a	
	10-50 years	13.2a	13.4a	14.3a	
	fire p value	0.44,0.91,83df	0.012,4.06,83df	0.15,1.82,83df	
July ¹	Mean ²	17.0 ± 0.2A	17.9 ± 0.2B	18.9 ± 0.2C	0.001, F=17.84, 282df
	1-3 years	17.1a	14.1b	19.1a	
	4-5 years	16.2a	14.7b	20.1a	
	5-10 years	17.7a	12.7a	18.2a	
	10-50 years	16.9a	12.6a	18.4a	
	fire p value	0.47,0.84,80df	0.006,4.76,80df	0.14,1.86,80df	
August ¹	Mean ²	16.6 ± 0.3A	16.9 ± 0.11B	17.9 ± 0.13C	<0.001, F=29.39, 393df
	1-3 years	17.0b	17.6b	18.2a	
	4-5 years	15.5a	17.0b	17.9a	
	5-10 years	16.5a	16.6a	17.4a	
	10-50 years	16.6a	16.4a	17.7a	
	fire p value	0.01,5.76,110df	0.01,6.72,110df	0.09,1.62,110df	

¹ Soil temperature was measured at a depth of 15 cm in the soil.

² Values are least squared means measured in degrees Celcius. Capital letters denote a significant difference (p=0.05 level) between slope position (bottom, mid slope, or top of ridge). Small letters denote significant differences (p=0.05 level) between temperatures of different years since the site was last burned using multiple contrasts based on Tukey. Order of probability is p-value, F statistic, and degrees of freedom.

Generally, the soils on our study sites were similar throughout the pothole slope with more organic material down next to the pond that is a result of plant production differences. Production capability differences seem to be water limited rather than nutrient limited. Carbon/nitrogen ratios indicate that plant characteristics are similar on the entire pothole slope, and organic breakdown is similar in these locations (Table 2.5).

Table 2.5. Soil properties of Lostwood soils by geographic position on the pothole pond slope.

Soil Factors	Bottom of hill	Mid Slope	Top of hill	P level ¹
Texture				
% clay	16 $\pm$ 2.0A	18 $\pm$ 2.0A	19 $\pm$ 2.0A	p=0.661, F=0.72, 30df
% sand	49 $\pm$ 4.3A	47 $\pm$ 4.3A	46 $\pm$ 4.3A	p=0.833, F=0.18, 30df
EC	456 $\pm$ 39.4A	411 $\pm$ 39.4A	508 $\pm$ 39.4A	p=0.231, F=1.53, 30df
PH	6.7 $\pm$ 0.23A	6.8 $\pm$ 0.23A	7.0 $\pm$ 0.23A	p=0.554, F=0.54, 30df
Carbon(%)	6.6 $\pm$ 0.40B	5.0 $\pm$ 0.4A	4.2 $\pm$ 0.4A	p=0.001, F=8.34, 30df
Nitrogen(%)	0.540 $\pm$ 0.04B	0.419 $\pm$ 0.04B	0.359 $\pm$ 0.04A	p=0.011, F=3.02, 30df
C/N ratio	12.8 $\pm$ 0.34A	11.7 $\pm$ 0.34A	11.6 $\pm$ 0.34A	p=0.063, F=3.02, 30df
Organic	11.6 $\pm$ 0.77B	9.1 $\pm$ 0.77AB	6.9 $\pm$ 0.77A	p=0.001, F=9.09, 30df

1. P level is the probability that there is a difference between topographic location (bottom, mid slope, or ridgetop). Values followed by the same letter are not significantly different. Values followed by different letters are significantly different at the p=0.05 probability level.

Community Contrasts

Plant Species Composition. We found species of short grass prairies on the ridgetops, mid grass prairies at mid slope, and plants of tall grasses prairies down on bottoms. Grass species restricted to the ridgetop were *Bouteloua gracilis* and *Koeleria macrantha* (Table 2.6). *Schizachyrium scoparium* grew on bottom and mid slope sites but was most common on mid slopes. *Symphoricarpus occidentalis* was found on all mid slopes sites, 64% of bottom sites, and on 36% of ridgetop sites. *Andropogon gerardi* and *Sparina pectinata*, species typical of tall grass prairie, were found most commonly on bottom sites. Many forb and shrub species were found on two topographic locations (eg. *Artemisia frigida*, *Anemone multifolium*, *Rosa*

woodsii, and *Potentilla arguta*). Generalists appeared on all three topographic positions (eg. *Poa pratensis*, *Stipa comata*, and *Galium boreale*).

Spring Biomass. We measured two components of spring biomass, standing dead and ground litter. Bottom sites had significantly ($p=0.05$ level) more standing dead ($132 \pm 61 \text{ g/m}^2$) than either mid slopes or ridgetops ($97 \pm 44 \text{ g/m}^2$ and $63 \pm 35 \text{ g/m}^2$). The length of time since the site was last burned had no significant effect on the amount of spring standing dead (Table 2.7). Bottoms had less ground litter than either mid slope or bottom sites but this difference is only moderately significant ($p \leq 0.08$, Table 2.7). Litter tended to increase with increased time since the last fire; however, this was only significant on ridgetops where the oldest ridgetop sites (10-50 years) had significantly ($p < 0.05$) more litter than more recently burned sites (Table 2.7).

End of Season Biomass. Bottom plots produced significantly greater total end of season standing standing crop ($268 \pm 51 \text{ g/m}^2$) than either mid slopes ($207 \pm 48 \text{ g/m}^2$) or ridgetops ($141 \pm 26 \text{ g/m}^2$) (Table 2.7). Mid slope and ridgetop total end of season standing crops were not significantly different from each other (Table 2.7). Fire history did not make a significant difference in total end of season standing crop on any topographic position.

Grass end of season standing crop increased from the bottom upslope (Table 2.7, $p=0.05$). Bottom sites averaged $172 \pm 64 \text{ g/m}^2$ compared to mid-slopes that averaged $106 \pm 76 \text{ g/m}^2$ compared to ridgetops which averaged $80 \pm 41 \text{ g/m}^2$. On bottom sites and ridgetops grass standing crops were greater immediately after a burn than was produced 10-50 years later. Burn history did not affect grass production at mid slope.

Forb end of growing season standing crop followed the same trends as grass species. Bottom sites averaged $73 \pm 53 \text{ g/m}^2$ compared to mid-slopes which averaged $50 \pm 36 \text{ g/m}^2$, and ridgetops which averaged $43 \pm 31 \text{ g/m}^2$ which were all significantly different from each other ($p=0.05$ level). We found no trends in forb standing crop due to fire history.

Table 2.6. Species list by topographic position. Species occurring at two or more sites are listed. Data is entered as the percentage (%) of the sites in which the species were present.

Species Name	Bottom ¹	Mid ¹	Top ¹
GRASSES			
<i>Bouteloua gracilis</i>			36
<i>Koeleria macrantha</i>			82
<i>Carex filifolia</i>	18		9
<i>Stipa comata</i>	64	91	91
<i>Agropyron smithii</i>	18	9	18
<i>Poa pratensis</i>	91	100	64
<i>Bromus inermis</i>	9	91	
<i>Schizachyrium scoparium</i>	9	36	
<i>Andropogon gerardi</i>	82	9	
<i>Spartina pectinata</i>	64	9	
FORBS			
<i>Potentilla arguta</i>		18	27
<i>Echinacea pallida</i>	9	27	36
<i>Artemisia fridida</i>	18	55	82
<i>Anemone patens</i>	36	55	82
<i>Achillea millifolium</i>	64	73	73
<i>Psoralea tenuiflora</i>	18	18	18
<i>Helianthus annuus</i>	9	36	18
<i>Artemesia ludoviciana</i>	9	55	9
<i>Astragalus crassiocarpa</i>	9	18	9
<i>Cerastium arvense</i>	9	18	9
<i>Sphaeralcea coccinea</i>	27	55	36
<i>Solidago speciosa</i>	64	91	45
<i>Galium boreale</i>	64	100	36
<i>Liatris aspera</i>	45	27	9
<i>Campanula rotundifolia</i>	27	36	
SHRUBS			
<i>Rosa woodsii</i>	9	91	45
<i>Elaeagnus comuntata</i>	36	45	27
<i>Symphoricarpus occidentalis</i>	64	100	36

1. Bottom of the hill is the vegetation next to the pothole pond. Mid is the steepest slope vegetation between top and bottom. Top is the vegetation on the ridgetops.

Table 2.7. Biomass components of northern prairie by topographic position on slopes and years since the site was last burned.

	Bottom	Mid Slope	Top	Topo p value	
Litter (g/m ²)					
Mean ¹	398 ±277B	274 ±178B	186 ±140A	0.08, F=2.82, 19df	
1-3 years	174a	67a	53a		
4-5 years	467a	372a	159a		
10-50 years	484a	287a	375b		
fire p-value	0.49, 0.82, 82	0.13, 3.18, 5	0.02, 9.43, 5		
End of Season Standing Crop (g/m ²)					
Mean ¹	268 ±51C	207 ±48B	141A±26	0.0001, F=81.94, 254df	
1-3 years	263a	205a	138a		
4-5 years	305a	202a	144a		
10-50 years	260a	200a	145a		
fire p-value	0.35, 1.20, 83df	0.44, 0.90, 82df	0.45, 0.24, 80df		
Overwintering (spring) standing crop (g/m ²)					
Mean ¹	132 ±61B	97 ±44B	63A±35	0.03, F=4.14, 21df	
1-3 years	174a	90a	41a		
4-5 years	125a	120a	72a		
10-50 years	105a	60a	68a		
fire p value	0.57, 0.62, 5df	0.33, 1.38, 5df	0.17, 2.63, 5df		
Grass	Mean ¹	172 ±64C	106 ±76B	80 ±41A	<0.001, F=80.70, 254df
	1-3 years	185b	97a	89b	
	4-5 years	185b	111a	93b	
	5-10 years	199b	117ab	84b	
	10-50 years	137a	91ac	62a	
	fire p value	0.003, 9.96, 83df	0.01, 4.34, 82df	0.05, 2.72, 80df	
Forb	Mean ¹	73 ±53C	50 ±36B	43 ±31A	<0.001, F=10.66, 254df
	1-3 years	58a	52a	33b	
	4-5 years	102b	55a	42b	
	5-10 years	53a	49a	33a	
	10-50 years	83b	52a	61b	
	fire p-value	0.02, 3.90, 83df	0.85, 0.29, 82df	0.002, 4.73, 80d	
Shrub	Mean ¹	23 ±28B	51 ±62C	17 ±20A	<0.001, F=11.60, 254df
	1-3 years	19a	55a	16a	
	4-5 years	18a	34a	9a	
	5-10 years	6a	36ab	19a	
	10-50 years	40b	55ac	22a	
	fire p-value	0.001, 6.48, 83df	0.002, 5.70, 82df	0.24, 1.52, 80df	

1. Means are least square means measured in grams/meter square. Capital letter denotes significant differences between topographic position on the hill ($p=0.05$ level). Small letters denote significant differences between years since last burned ($p=0.05$ level) for that component using multiple contrasts (Tukey).

Topography did affect shrub end of season standing crop. Mid slope plots produced significantly more shrub standing crop ($51 \pm 62 \text{ g/m}^2$) than did either ridgetop ($17 \pm 20 \text{ g/m}^2$) or bottoms ($23 \pm 28 \text{ g/m}^2$). Bottom plots were affected by burn history. Old sites (time since burn) produced significantly more shrub standing crop than younger (shorter time since last burned) sites. Burn history did not affect end of season standing crop on ridgetops or mid slopes.

Phenology

We used NDVI as an index of phenology of prairie vegetation types. NDVI is plotted against season for each type (Fig 2.1). It is low (near 0) early in the season increasing to a maximum of 0.89 around July 1 (Fig. 2.1). During the remainder of the season it falls to 0.25 in late fall (Fig. 2.1). The rise in spring is associated with increasing biomass (cell wall structure, van Leeuwen & Huete 1996; Goodin & Henebry 1997). The decline in fall is associated with cell/chlorophyll death (reduced red absorption, van Leeuwen & Huarte 1996; Wessman et al. 1997). The seasonal course of NDVI among prairie types is parallel with published observations in tall, mixed, and short grass of the Great Plains (Ode et al. 1980; Paruelo & Laurenroth 1995; Goodin & Henebry 1997).

The seasonal pattern of plant condition (NDVI) might be caused by seasonal changes in temperature, water, or daylength. We made graphical and statistical tests of the season hypothesis. Figure 2.1 graphically associates NDVI with trends in soil temperature and soil water. The data were used to create a regression model predicting NDVI from measures of soil temperature, soil water, seasonal day, and seasonal day squared. Soil temperature and day (daylength) were correlated with NDVI season long (Table 2.8). Soil water is poorly correlated ($p=0.88$), perhaps because water stress only appears in late summer.

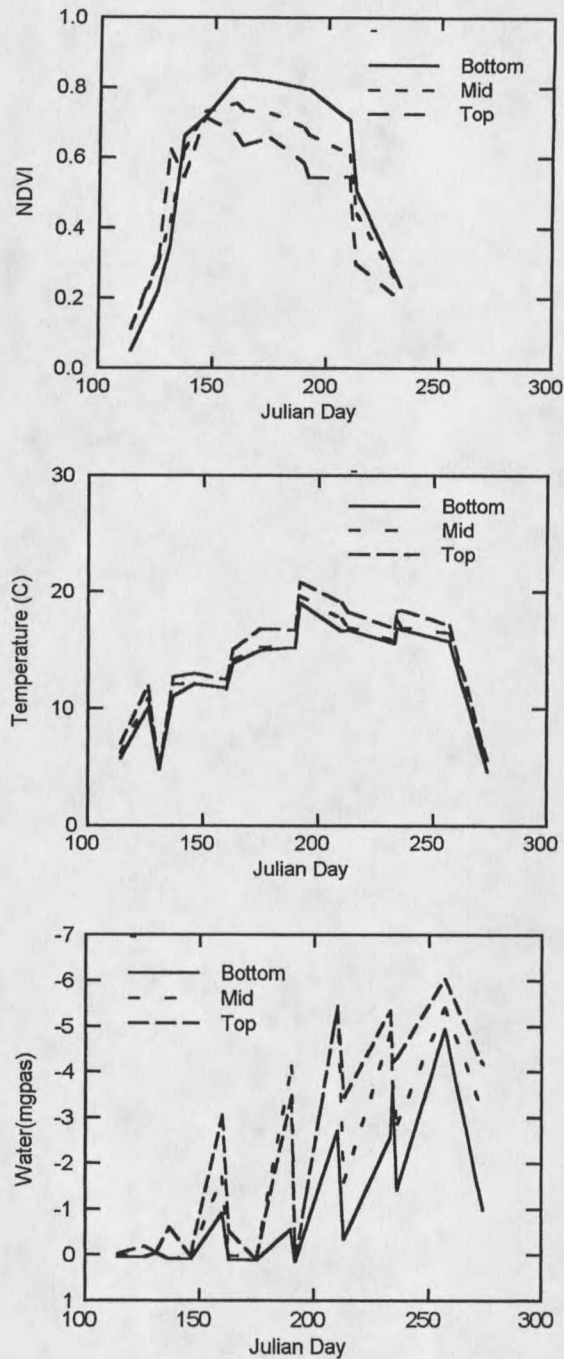


Fig 2.1. NDVI, temperature, and soil water over the growing season (Julian day). Three topographic positions include bottom (sites next to the pond), mid (mid-slope sites), and top (ridgetop sites).

Table 2.8 . NDVI over the season by topographic position. Environmental measurements are day of season (Julian Day), soil temperature(°C), and soil water (megapascals).

	Coefficient	p value
Constant	-5.087	0.001
Temperature ¹	-0.016	0.001
Water ¹	-0.0035	0.877
Julian Day	0.069	0.001
Day*Day ²	0.00019	0.001
model adjusted R ² =0.78		

1. Soil temperature and soil water measured 15 cm below the soil surface
2. Quadratic effect produced by multiplying Julian day times Julian day

Discussion

Vegetation

The refuge's location on the Missouri Coteau, give it a ridged and pitted topography with diverse environments and several azonal vegetation types in addition to the zonal mixed grass type. Moving up a slope one might pass through pond water, cattails or bulrushes, tall grass, mixed grass, and short grass. We studied the upper three zones. Bottom sites are dominated by tall grasses and forbs (*Andropogon gerardi*, *Spartina pectinata*, *Solidago* spp. *Liatris aspera*, *Psoralea tenuiflora*, and *Galium boreale*). Mid slope sites are dominated by clumps of *Schizachyrium scoparium* in a matrix of *Poa pratensis* and *Stipa comata* and many forb (eg. *Achillea millifolium*, *Anemone patens*, *Helianthus annuus*, *Solidago* spp) and shrub (especially *Symphoricarpus occidentalis*) species typical of mixed grass prairie (Weaver & Fitzpatrick 1934, Weaver 1968; Simms & Risser 2000). Grass species such as *Bouteloua gracilis* and *Koeleria macrantha*, typical plants of the shortgrass prairie (Weaver 1968; Bragg and Steuter 1996; Sims & Risser 2000) were found on ridgetops (Table 2.6).

Environmental Control

1) One expects soils to vary little on the topographic gradient because morainal material is well mixed and post-glacial time is inadequate for significant development (Coupland 1950). Physical and chemical characteristics support this expectation. Soils on our sites were sandy (46-53 %) and topographic position did not affect soil texture (Table 2.5, $p=0.622$). Soil pH did not vary significantly (Table 2.5, $p=0.886$). Electrical conductivity, an indicator of salinity, did not vary significantly (Table 2.5, $p=0.448$). Where vegetation varies with topography, it is expected to modify the organic characteristics of the underlying soil. Thus soil carbon and nitrogen content were highest on more productive bottom sites (Table 2.5, $p=0.006$ & $p=0.024$). Schimel et al (1985) observed similar increases and attributed them to either productivity differences or movement. While our carbon/ nitrogen ratios did not vary on the gradient ($p=0.121$), Schimel et al (1985) reported increases downslope. A constant C/N ratio suggests a constant decomposition rate while increases in C/N ratio suggest a decomposition rate lowered by cooler or wetter soils downslope. We conclude that soil variation on the topographic gradient is slight and more likely controlled by vegetation type than the topographic gradient controlling the soil variation.

2) Differences in soil temperature might determine the topographic distribution of vegetation. Soil temperatures on hill tops are about 1C warmer than those in bottoms in April-August (Table 2.4, $p=0.05$) and about 1C warmer than mid-slope sites in June, July and August (Table 2.4, $p=0.05$). Because topographic temperature differences are so small relative to latitudinal variation in temperature in tall, mixed or shortgrass prairies (Weaver & Fitzpatrick 1934; Knapp et al 1993; Briggs & Knapp 1995) we doubt that the temperature differences are biologically significant.

3) Differences in water availability might determine topographic variation in vegetation. The possibility of such differences was examined by comparing soil water at 15 cm under tall, mixed, and shortgrass plots. There were no differences in April and May, uplands (slopes and hilltops) were drier in June ($p < 0.05$), uplands were drier in July ($p < 0.05$) and hilltops were drier than both bottoms and slopes in August ($P < 0.05$). Despite equivalent rainfall, water availability might decrease upslope for at least four reasons. First, water runs off uplands (the existence of ponds demonstrates this). While surface soils in the bottoms are relatively dry in August tallgrass plants may be sub-irrigated with pond water (water at 50cm in

bottoms=-0.085 megapascals). Snow blows off uplands (Table 2.3) and especially where recent burning has removed standing dead 'snowfences'. We speculated that there was an evaporation difference between topographic levels. Even if subsoil water were adequate throughout the gradient, stress might be greater on upland (shortgrass) than bottom (tallgrass) sites if windflows induced greater evapotranspiration rates on upland sites. While we expected significantly higher loss rates on upland sites, we couldn't demonstrate a difference with our evaporimeters (Table 2.3, $p=0.85$). Soil water was not a limiting factor from late April until mid July on any site (Table 2.2). Ridgetop production was limited by shortages of water, at least in the top 15cm of soil, in late July and most of August (Table 2.3). Mid slope had shorter periods of soil water shortage that most likely limit these plants as well. Bottom sites were never water limited.

Composition and Structure

Composition. While measurement of community composition and structure were not central to our project, we offer the following observations on composition. Grass (6-8 species), forb (14-15 species), and shrub (3 species) richness(number of species) are topographically similar (Table 2.6). The fraction of biomass contributed by forbs is similar across the gradient (34-39%). The shrub's proportion of current production is similar across the gradient (14-16%). While end-of-season standing crop correctly represents the contribution of grasses and forbs to community composition, measurements of current production (leaves and new twigs) considerably understates the contribution of shrubs (Table 2.6).

Production and decomposition . End of season standing crops decreased with each step ($p=0.05$) on bottom, slope, and ridge sites (268 ± 51 , 207 ± 48 , and 141 ± 26 g/m²). Throughout the Great Plains tallgrass prairie sites average 368 ± 123 g/m² annual production (Weaver 1924; Kelting 1954; Old 1969; Knapp 1984; Abrams et al. 1986; Engle et al. 1988; Briggs & Knapp 1995;), mixed grass prairie sites average 247 ± 109 g/m² (Weaver 1924; Kelting 1954; Peet et al 1975; Rice & Parenta 1978; Abrams et al. 1986; Engle et al. 1988; Briggs & Knapp 1995; Peltzer et al 1998; Esrichsen-Arychuk et al 2002), and shortgrass prairie average 144 ± 95 g/m² (Smoliak 1956; Engle et al. 1988; Milchunas et al. 1988; Peltzer et al. 1998).

Production is countered by decomposition; our data speak to three aspects of this little discussed process. 1) Decomposition may also have a seasonality (phenology). Belowground, conditions are sufficiently moist to support decomposition during most of the year. Aboveground, decomposition probably occurs under snow and on uplands it must occur during the rainy season (April-June, Weaver 1985). In both cases, nutrients tend to be delivered to plants in the season of greatest need (Weaver and Forcella 1979). 2) Production without decomposition would result in rapid litter accumulation. Thus subtracting the litter accumulation rate for stands unburned in ten years from production (Table 2.6) provides approximate decomposition rates for the three ecosystems considered. Because litter accumulation rate is near zero 5-50 years after a fire (Table 4.1, Fig 4.1) decomposition rates from bottoms to ridges must be similar to production rates ($268\text{g/m}^2/\text{yr}$, $207\text{g/m}^2/\text{yr}$, and $141\text{g/m}^2/\text{yr}$). 3) C/N ratios of litter ($\text{C/N}=36.3$) and end of season forage ($\text{C/N}=34.8$) were very similar ($t=0.068$, $p=0.51$ with 20df). C/N ratios of production and litter were equal across the topographic gradient. If cellulose was decomposing faster in one type than another type of vegetation, nitrogen would concentrate in the litter of the site that is decomposing faster; however, C/N ratios are not different which suggests that decomposition rates are equal across the topographic gradient which we know is not true because litter would continue to increase on bottoms. Our litter measurements show that litter on bottoms and midslope do not continue to increase (Table 2.7).

Phenology

We expected the season of production to vary among prairie types/topographic zones, beginning earlier on uplands and lasting longer in bottoms. We tested this hypothesis with repeated measures of an index (NDVI, see methods) of photo-synthetically active material. Greening of Choteau vegetation began in late April, increased sharply, and approached its maximum in late May. Browning increased strongly in mid-July, and was nearly complete by early September (Fig 2.1). Except for the early season spike in ridge grassland reflectance, the progression was similar throughout the gradient. Phenology observed in the plains was similar, even down to the pre-season spike in greening unique to short grass prairie (Goodin & Henebry 1997). While the seasonal progression of phenology was similar across the topographic gradient, the intensity of summer reflectance fell from tallgrass through mixed grass to shortgrass prairie. This is surely

due to differences in reflective surface, as indexed by standing crop (Table 2.7) and has been reported at the geographic scale in short, mixed and tall grass prairies (Goodwin and Henebry 1997; Tieszen et al. 1997).

Community phenology might be controlled by seasonally limiting factors (eg. temperature or water) or to a dependable predictor of their levels (eg. daylength). 1) One speculates that greening in spring is determined by temperature, because it occurs as soil temperatures rise (Fig 2.1) from limiting levels to non-limiting levels (5C-15C, Larcher 1995), while water levels remain constant at non-limiting levels (Fig. 2.1, Larcher 1995). 2) The browning of late summer and fall is likely induced by falling temperature because both browning and cooling begin in mid July particularly for mid slopes and ridges. Soil water availability is not as well correlated since water stress levels are not reached until early July before browning begins (Fig 2.1). The poorer correlation may be an artifact of measuring soil water at 15 cm; water stored in deeper layers (despite their sandiness, Table 2.5) may be sufficient to maintain water levels till mid July. 3) Greening and browning might be controlled by a trigger factor (light) rather than resource limits (temperature or water). Grasses have likely evolved mechanisms to detect shortening daylength as a trigger for preparation for stressful seasons, for example, to allow plants to fruit and transport carbohydrates and minerals to roots before drought kills shoots and prevents the process (Larcher 1995).

Fire Effects

We expected fire to reduce woody plant presence because burning should destroy the woody plants and allow fire resistant grasses and forbs to dominate the sites (Risser et al 1981; Walter 1984; Axelrod 1985; Collins 1987; Anderson 1990; Collins & Gibson 1990; Simms & Risser 2000). While shrub presence in the landscape obviously increases with increasing time-since-fire, we did not sample to demonstrate the change. Minimal support for this otherwise un-quantified increase in shrub dominance with time is provided by the fact that shrub production increases with time-since-fire on bottom sites (Table 2.7). First, because we intended to compare grasslands, we under-sampled shrubs at long-unburned sites by sampling between woody (*Symphoricarpos* and *Shepherdia*) clones. Second, data gathered to measure productivity are poorly adapted to demonstration of dominance. While presence of grass and forb components are indexed well by mass of new growth, new growth of shrubs (leaves and twig tips) omits a major part of shrub component (stems and trunks).

Conclusions

Tall grass (bottom), mixed grass and shortgrass (top) prairie are tightly juxtaposed at Lostwood NWR. We take this opportunity to compare the systems with respect to composition, structure, function, response to fire and environmental requirements in a single climate. Despite changes in dominant species, species richness and dominance, are little changed. Spring greenup and fall browning differ little on the topographic gradient, though reflectance [NDVI] decreases from bottom to top sites. Productivity decreases upslope, in parallel with reflectivity. Decomposition rates decrease upslope with decreasing productivity. Time of spring greenup and fall browning differ little on the topographic gradient. Controls for topographic changes are probably not soil quality, temperature, evapo-transpiration, or fire; soil water availability is the best candidate as we hypothesized. Controls for phenologic change are likely temperature/day-length in spring and drought/ daylength in the fall.

Future topics to investigate include seasonal effects such as day-length and water drainage which would include water table levels. Species composition also needs to be more intensively studied. Removing biomass components over longer periods may change some of its effects on the vegetation (our study covered only three years)

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CHAPTER 3

FUEL LOADS IN TALL, MIXED, AND SHORTGRASS VEGETATION

Introduction

Fuel loads are well studied in forests (Spies et al. 1988; McComb & Lindenmayer 1999), but are rarely studied in grasslands. Fire managers use fuel load information as one factor to predict fire behavior (Ewing & Engle 1988; Whelan 1995), to predict effects of fire on vegetation and soil (Bragg 1982; Ewing & Engle 1988), and to estimate airborne effluents (McNaughton et al 1998). The two major components of fuel loads are standing material (dead and living) and litter. Standing crop also provides forage and shelter to domestic and wild animals, small organisms such as microarthropods (Arenz & Joern 1996), birds (Herkert 1994; Kruse & Bowen 1996), and small mammals such as mice, shrews, and prairie voles (Clark et al. 1989; Whelan 1995), pocket gophers (Hobbs & Mooney 1991) , and badgers (Weaver & Fitzpatrick 1934).

The objectives of this work were to compare fuel loads in tall, mixed, and shortgrass prairie. Two complementary data sets were studied. First, we studied fuel loads with harvest methods on paired moist, mid-slope, and dry sites in a single climate (NW N Dakota). Second, because our North Dakota sites (bottom, mid slope, and upland) share species composition with tall (*Andropogon gerardi* & *Spartina pectinata*), mixed (*Shizachrium scoparium* & *Stipa comata*), and short (*Bouteloua gracilis* & *Stipa comata*) grass prairies, we used published data to compare fuel loads in grasslands of the plains with their North Dakota counterparts. We addressed four questions. 1) What are fuel loads in major grasslands? 2) How do fuel loads in short, mixed, and tallgrass types on the Missouri Coteau differ from the general cases in these prairie types? 3) How does time since fire affect fuel loads? 4) How does simulated grazing affect fuel loads?

Methods

We measured variation in fuel loads with topography, time since burning, and biomass removal (simulated grazing) in grasslands in NW North Dakota, specifically on the Lostwood National Wildlife Refuge near Stanley, ND. The refuge lies on the terminal moraine of the last continental glaciers (Missouri Couteau) which gave the area a rolling topography consisting of undrained basins, slopes, and hilltops (Pielou 1991; Richardson 2000).

Fuel loads on our N. Dakota sites are expected to decline upslope because bottomland sites are moister/richer than wind exposed hill-top sites. Producer composition shows bottom, slope, and upland sites at Lostwood NWR are similar to tall (*Andropogon gerardi* & *Spartina pectinata*), mixed (*Schizachrium scoparium* & *Stipa comata*), and short (*Bouteloua gracilis* & *Stipa comata*) grass prairies of the Great Plains. To test this hypothesis we compared fuel loads on bottom, slope, and upland sites on nine transects.

We expected fuel loads to increase as time since fire increases. While current production was not changed by fire history, we expected litter to accumulate as time since fire increased, and therefore for the aggregate to increase (Table 3.1). To test this hypothesis we chose transects which were unburned for two(1), three(1), four(3), five(1), twelve(1), and over fifty (2) years.

Grazing might gradually reduce current production as the grazers remove nutrients and change the species composition of the community (Noy-Meir 1978; McNaughton 1979, 1993; Biondini & Manske 1996; Savory 1999). To examine this possibility we compared production in plots with three levels of simulated grazing. We installed three experimental plots at each of the three topographic levels (bottom, mid slope, and hill top) at the nine transects (representing different fire histories, Table 3.2) for a total 81 plots. The 3X4 meter plots were located adjacent to each other on the contour and one meter apart. The three levels of simulated grazing were no removal (no grazing), spring removal of all standing crop in three consecutive years (moderately grazed), and spring removal of both standing dead and litter in three consecutive years (heavy grazing). After the plots were staked, a treatment was randomly assigned to each plot. While these treatments simulate the effects of grazing on fuel loads (Dix 1960; Sims and Singh 1978; Shuman et al. 1999; Biondini et al 1998), they do not attempt to mimic other affects of grazing such as

herbivore selectivity and repetitive consumption (Stoddard & Smith 1943; Coughenour 1985; McNaughton 1986, 1979; Savory 1999).

Methods used to estimate end of season standing crop, spring standing crop, and litter follow. 1) End of season standing crop was measured in all 81 plots (9 treatments x 3 topographic positions x 3 grazing treatments) in late August 1998, 1999, and 2000. Standing crop was estimated by harvesting biomass from two 30 x 60cm quadrats; separating it into grass, forb, and shrub; drying; weighing; and adjusting masses to the square meter basis. 2) Spring standing crop was measured in twenty seven plots (9 transects x 3 topographic positions) in 1999. Standing dead was removed from the 'heavily grazed' plot by mowing to 3cm with a weed whip, and carefully raking with a broom rake to gather all litter. The litter was bagged, weighed wet, reduced to dry weight by multiplying by a dry weight/wet factor. This factor was determined by weighing approximately 10% of the sample wet, drying, and reweighing. This weight was further reduced by removing soil; approximately 25% of the sample was ground and a sub sample was ashed (550C for 6 hours), a soil removal factor was calculated as (litter-ash)/litter, and litter dry weights were multiplied by this factor. 4) Large plots were used for estimation of standing dead and litter quantities because the experimental plots had to be cleared anyway, because this minimized edge effect, and because most variation in the site was included. End of season standing crops were harvested in smaller plots to yield manageable quantities and to minimize disturbance in the un-grazed treatments.

Carbon and nitrogen available for vaporization in fire (Table 3.3) were determined by multiplying standing crops measured above (Table 3.1) by carbon and nitrogen contents of end-of-season standing crop and litter measured on sub-samples. Approximately 2.5% of the material collected (ie. 35% of the 10% used for the water content measurement) was ground to 1mm in a Wiley mill and thoroughly mixed. A 0.2 gm sample of this was analyzed by the MSU Soil Testing Lab with a LELCO 2000 CNS combustion analyzer (Nelson & Summers 1996; Bremner 1996). While carbon and nitrogen concentrations are not reported directly, they can be calculated by dividing C and N availabilities (Table 3.3) by forage quantities reported (Table 3.1).

Results

Fuel was calculated as the sum of two components (litter and standing crop) in two seasons (spring=minimum estimate and late summer=maximum estimate), three topographic positions (bottom, midslope, and hilltop), and increasing time since the site was cleared by fire. Vegetation dominance on the topographic (moisture) gradient shifts from species from the tallgrass prairie (*Andropogon gerardi* and *Spartina pectinata*), to the mixed grass prairie (*Schizrachium scoparium*, and *Agropyron smithii*), to the short grass prairie (*Bouteloua gracilis* and *Stipa comata*).

Average litter quantities fell from rich bottomlands through slopes to dry uplands (bottoms=398 $\pm$ 278 g/m², slopes=274 $\pm$ 178 g/m², and hilltops= 186 $\pm$ 140 g/m², Table 3.1). On the same sites litter seemed to accumulate with time since burn. In the richer environments (bottom and mid-slope) litter amounts rose from the lowest level soon after fire (Table 3.1) to an equilibrium level approximately five years after the site burned. On hilltop sites litter continued to accumulate higher litter amounts throughout at least the first 50 years after fire occurred (Table 3.1). The topographic trend is significant (p=0.05 level) with decreasing litter as one moves up the slope. The apparent trend of accumulation of litter through time was not statistically significant.

End of season standing crop, mostly current production, also decreases from rich bottom sites through mid slopes to uplands ($\bar{x}$ =268 $\pm$ 52, 207 $\pm$ 48, and 141 $\pm$ 26 g/m²) with biomass falling significantly at each topographic step (Table 3.1). Total standing crop was not affected by burning history (Table 3.1). The third dimension in this experiment examined the effect of removing litter and standing crop of the previous season.. We did not find any evidence that removal of standing crop (simulated grazing) , or standing crop and litter affected total end of season standing crop (Table 3.2).

Spring standing dead is the weathered product of end-of-season standing crop from the previous year. Masses declined from bottom sites upslope to dry upland sites (132 $\pm$ 61, 97 $\pm$ 44, and 63 $\pm$ 35 g/m²), with standing crop significantly higher on bottoms and slopes than on upland sites (Table 3.1). As expected from the lack of trend in end of season standing crop with fire treatment, we found no trend in the amount of spring standing dead (Table 3.1). The fraction of end-of-season standing crop surviving the winter changed little from bottom sites to mid-slopes and windswept hilltops (50%, 47%, and 46%).

Table 3.1. Effects of topography and fire history on standing crop components.

Biomass Components	Bottom	Mid Slope	Top	topographic p value
Litter (g/m ²)				
Mean ¹	398 ±277B	274 ±178B	186 ±140A	0.08, F=2.82, 19df
1-3 years	174a	67a	53a	
4-5 years	467a	372a	159a	
10-50 years	484a	287a	375b	
fire p-value	0.49, 0.82, 82	0.13, 3.18, 5	0.02, 9.43, 5	
End of Season Standing Crop (g/m ²)				
Mean ¹	268 ±51C	207 ±48B	141A±26	0.0001, F=81.94, 254df
1-3 years	263a	205a	138a	
4-5 years	305a	202a	144a	
10-50 years	260a	200a	145a	
fire p-value	0.35, 1.20, 83df	0.44, 0.90, 82df	0.45, 0.24, 80df	
Overwintering (spring) standing crop (g/m ²)				
Mean ¹	132 ±61B	97 ±44B	63A±35	0.03, F=4.14, 21df
1-3 years	174a	90a	41a	
4-5 years	125a	120a	72a	
10-50 years	105a	60a	68a	
fire p value	0.57, 0.62, 5df	0.33, 1.38, 5df	0.17, 2.63, 5df	
Spring Fuel (overwintering plus litter)				
Mean ¹	530 ±303B	371 ±197B	250 ±157A	0.06, F=3.01, 30df
1-3 years	349a	157a	94a	
4-5 years	592a	491a	231a	
10-50 years	589a	346a	443b	
fire p-value	0.69, 0.40, 5df	0.13, 3.11, 5df	0.04, 6.63, 5df	
End of Season Fuel (EOS plus litter)				
Mean ¹	692 ±339B	471 ±200B	201 ±157A	0.02, F=4.37, 30df
1-3 years	443a	286a	159a	
4-5 years	764a	568a	212a	
10-50 years	798a	465a	223a	
fire p-value	0.51, 0.77, 5df	0.30, 1.53, 5df	0.50, 0.81, 5df	

1. Means are least square means measured in grams ±standard deviation/meter square. Capital letter denote significant differences between topographic position on the hill (p=0.05 level). Small letters denote significant differences between years since last burned (p=0.05 level) for that component.

Table 3.2. Effect of simulated grazing on end-of-season standing crop (g/m^2 , $\bar{X} \pm \text{sd}$) Average of three years.

	Bottom	Mid Slope	Top
<i>Grazing treatment</i>			
No harvest ¹	274 $\pm$ 89a	224 $\pm$ 64a	150 $\pm$ 48b
Std crop harvested ¹	264 $\pm$ 89a	198 $\pm$ 67a	134 $\pm$ 52a
Sc & litter removed ¹	276 $\pm$ 89a	179 $\pm$ 64a	137 $\pm$ 48a
Grazing p-value	0.78, 0.24, 84df	0.18, 1.76, 83df	0.35, 1.04, 81df

¹ End of season standing crop is compared on plots from which nothing was removed, spring standing crop was removed, and both spring standing crop and litter were removed. Comparisons were made in autumn 2000 after the third summer of harvesting.

2. Different lower case letters in a column indicate significant differences in yields between treatments. Order of p values are p value, F statistic, and degrees of freedom(df).

Table 3.3. Carbon and nitrogen available in litter and standing crop components for vaporization in prairie fires (gm/m^2). Stands analyzed were 4-50 years old.

	Bottom	Mid Slope	Top	p-value
<i>Carbon</i>				
Litter	124 $\pm$ 28.7a	132 $\pm$ 28.7a	66 $\pm$ 30.4a	p=0.25, F=1.49, 23df
EOS std crop ¹	132 $\pm$ 6.9b	87 $\pm$ 6.9a	56 $\pm$ 7.3a	p<0.01, F=29.06, 49df
Total EOS fuel ¹	260 $\pm$ 33.8b	226 $\pm$ 33.8ab	124 $\pm$ 35.8a	p=0.03, F=4.05, 23df
<i>Nitrogen</i>				
Litter	3.73 $\pm$ 1.21a	4.74 $\pm$ 1.21a	2.19 $\pm$ 1.28a	p=0.36, F=1.05, 23df
EOS std crop ¹	3.59 $\pm$ 0.21c	2.69 $\pm$ 0.21b	1.70 $\pm$ 0.23a	p<0.01, F=18.30, 49df
Total EOS fuel ¹	7.43 $\pm$ 1.3a	7.53 $\pm$ 1.3a	3.91 $\pm$ 1.4a	p=0.13, F=2.25, 23df

¹ Biomass components are compared on three different positions on the slope. Litter estimates were made in Spring 1999. End-of-season (late August) measurements are an average of three years (1998, 1999, and 2000).

Table 3.3 gives estimates of carbon and nitrogen losses on the three prairies that may be lost from the system if these components are burned.

Spring fuel is the sum of litter and spring standing dead. 1) Since both components decline significantly upslope one expects fuel loads to decrease upslope, but while fuel loads do decrease upslope from the bottom ($530 \pm 303 \text{ g/m}^2$) to mid slope positions ($371 \pm 197 \text{ g/m}^2$), the difference is statistically insignificant ($p=0.06$). Fuel loads on hilltops ($250 \pm 157 \text{ g/m}^2$) are significantly less than in the lower positions ($p=0.05$ level). 2) While standing crop does not change with years since fire, the measurable

accumulation of litter through time creates a trend of decreasing fuel load upslope in which upland loads are significantly less than on bottom or slope sites ($p=0.05$ level).

Fuel available in late summer is the sum of litter, seasonal production, and perhaps a little spring standing dead. 1) Since the primary components decrease upslope autumn fuel must decrease significantly (692 ± 339 , 471 ± 200 , and 201 ± 157 g/m²). Again, while fuel decreases significantly from the bottom and slope sites to ridges, but fuel loads on the lower slope positions are not significantly different from each other ($p<0.05$ level, Table 3.1). 2) Litter and summer production both contribute to late summer fuel. Production varies little with time since the last fire, but litter accumulates significantly. Therefore, litter accumulation is responsible for the increase in fuel with increasing time since fire only on the ridges (Table 3.1). 3) The composition of the end of season fuel averages 57% grass, 27% forb, and 15% shrub on periodically burned sites. On bottomland sites grass is slightly more important (64%) and it may tend to exclude shrubs (9%). We observed no trends in composition with time since fire.

Data for parallel comparisons of dry to mesic grasslands of the Coteau with short, mixed, and tall grass prairies of the Great Plains was gathered from published literature (Table 3.4). While these data paint a general picture they cannot be pushed too far because studies recorded different components. It is sometimes unclear exactly what was measured and what stratification that was used (eg. Geography, grazing level, and fire treatment). We cautiously compared fuel and fuel components averaged within three prairie types (short, mixed, and tall grass), three grazing levels (ungrazed, grazed, and heavily grazed), and two fire treatments (burned and unburned).

Discussion

The Setting

Common dominant species show the role of topographic similarity of Coteau grasslands to tall grass (*Andropogon gerardi* & *Spartina pectinata*), mixed grass (*Schizrachrium scoparium* & *Stipa comata*) and shortgrass (*Bouteloua gracilis* & *Stipa comata*) prairies communities of the Great Plains (Kuchler 1964). Therefore, comparisons of biomass components on topographic zones on the Missouri Coteau and on

longitudinal/precipitation zones in grasslands of the Great Plains should illuminate discussion of fuel loads in both spheres. The data used in making each comparison is indicated for the reader's scrutiny (Table 3.4).

Fuel loads

Since standing crop varies seasonally, its dynamics are described with seasonal maxima (end-of-season standing crop) and minima (spring standing crop). 1) Litter masses in Coteau stands unburned for over four years (476, 330, and 267 g/m², Table 3.1) were similar to published values from tall, mixed and shortgrass prairies (582, 332, and 145 g/m², Table 3.4). 2) Autumn standing crops on bottom and slope positions (241 and 198 g/m², Table 3.1) were considerably less than in tall and mixed grass prairie (476 and 368 g/m², Table 3.4). However, standing crops were similar on ND hilltops (141±26 g/m²) and shortgrass prairie (136 g/m²). 3) The tendency of Coteau grasslands to have more litter per unit of production (1.98, 1.67, 1.89 equilibrium litter/EOS standing crop) than grasslands of the plains (1.07, 0.90, and 1.22) may reflect a trend toward lower decomposition rates on northern sites . 4) Summing litter and autumn standing crop to get autumn fuel loads shows lower loads on the Coteau (bottom=781 and slopes= 517 g/m², Table 3.1) than in plains to the south (tall grass=1048 g/m² and mixed grass=701 g/m²).

In contrast fuel loads on Coteau hilltops (414 g/m²) are larger than those in the shortgrass prairie (282 g/m², Table 3.1). These summer fuel loads are reduced by factors such as wear of winter, fire, and herbivory. The effects of these factors are reviewed in these paragraphs. First, comparison of our measurements of spring (overwintered) standing crop with the maximum standings crop of the previous August demonstrates the effect of weathering. Our litter component was measured in the spring and presumed unchanged throughout the summer. Spring standing crop (end-of-season standing crop minus overwintering loss) averages on the Coteau were 132 g/m² on bottom sites, 97 g/m² on slopes, and 63 g/m² on hilltops (Table 3.1). Overwinter losses were similar across the topographic levels (50%, 47%, and 46%).

Second, students following burns in the tallgrass prairie observed either no decrease (Willms et al. 1993; Wessman et al. 1997) or slight increases in production (Table 3.4). Increases appear when heavy litter loads are burned and may result from the fertilizing effect of ash components (Hadley & Kieckhefer 1963; Old 1969; Hulbert 1988; Briggs & Knapp 1995).

Third, one expects standing crops to decrease with grazing both because material that otherwise contributes to standing crop and litter components is removed and because plants are weakened in cases where nutrients are exported from the system. Published data from the Great Plains (Table 3.4) used positive and negative deviations of grazed from ungrazed yields expressed as grazed standing crop/ ungrazed standing crop (tallgrass= 69%, mixed grass=74%, & shortgrass= 111%,) and heavily grazed standing crops from ungrazed (tallgrass= na%, mixed grass=45%, & shortgrass= 71%). Litter is generally reduced by grazing (Table 3.4) in grazed / ungrazed prairie sites (tallgrass=69%, mixed grass=38%, & shortgrass=92%) and ungrazed versusd heavily grazed (shortgrass=65%). The resultant effects of grazing on fuel loads (Table 3.4) are reductions in shortgrass (101% and 67 % of ungrazed), mixed grass (65 and 43%), and tall grass (94 and na %). Heavy grazing on a moister mixed grass prairie at the same latitude reduced litter by 99% and fuel by 51% (Biondini et al. 1998).

Effects of mechanical removal of material from Coteau grasslands were less than expected. Removal of litter obviously reduced this component and therefore reduced total fuel. However, in our three year experiment end-of-season standing crop was not affected by removal of either litter and/or standing crop (Table 3.3). As a result, we expect no short-term reduction in production from removals such as haying. While one might expect a decline in longe term removals due to export of nutrients, such reductions have not been shown in longer term studies (Weaver & Fitzpatrick 1934; Weaver & Rowland 1952).

Volatilization of carbon and nitrogen

Fire in these grasslands will release carbon (CO_2) to the atmosphere in proportion to the acreage of each vegetation type burned, the biomass present per unit area, and the completeness of combustion. Carbon contents of the components (Table 3.3) are litter (66-132 g/m^2), forage (56-132 g/m^2) and total fuel (124-260 g/m^2). Experimental combustion varies from 85-99% in tall grass prairie (Bragg 1982) and 75% in intensely burned tropical savannas (McNaughton et al. 1998) down to 20% in low intensity fires in savannas (McNaughton et al. 1998).

Fire simultaneously de-fertilizes burned sites. Nitrogen available for release (Table 3.3) is approximately; litter (2.19-4.74 g/m^2), forage (1.70-359 g/m^2), and total fuel (3.9-7.5 g/m^2). Nitrogen release may be 10-80% and may not parallel carbon loss because highly flammable leaves are richer in

nitrogen than are the less flammable stems (McNaughton et al. 1998). In these grasslands losses will depend on reserves (greatest in bottoms, Table 2.3) and burning characteristics with higher rates of loss on upland sites (sites with fine stemmed vegetation and light litter) and lower rates of loss in bottoms (sites with coarser stems and heavier litter).

Table 3.4. Fuel loads in North American grasslands.

state	pptn	note	prod	std	p+ sd	litter	litt+ sd	fuel	authority
<i>Shortgrass prairie</i>									
General	-	-	-	-	0-150?	-	-	-	Sala 1988
Alberta	198	-	376	-	-	-	133	509	Dormar 1997
Sask	384	-	-	-	112	159	-	273	Wilson 1993
Mont	307	agsm	-	-	128	-	-	-	Weaver 1983
	298	bogr	-	-	105	-	-	-	Weaver 1983
S Dak	390	excell	-	-	160/27	75/13	-	235	Weltz 2000
	"	fair	-	-	45/14	25/10	-	70	
Wyo	365	-	73	45	118	38	83	156	Redente 1989
	384	lt-hv	112/36	(=values, lt-heavy)	-	-	-	-	Manley 1997
Colo	-	-	-	34	-	-	-	-	Detling 1979
	-	?	77-150	0-82	-	8-20	-	-	Laing 1989****
	-	graz	77-150	51-86	-	0-0	-	-	
	220	ungr	105	35	140	177	212	317	Sims 1978
	"	graz	97	37	134	128	165	262	
	220?	ungr	-	-	131/13	143/32	-	274	Hart 1998
	"	graz	-	-	105/15	26/13	-	131	
	350	good	-	-	101/28	189/135	-	236	Weltz 2000
	"	fair	-	-	75/26	157/71	-	232	
	384	ungr	133	47	180	287	334	467	Schuman 1999
	"	light	122	49	171	165	214	336	
Texas	300	ungr	103	96	199	232	328	444	Sims 1978
	"	graz	119	79	198	215	294	413	
	375	fair	-	-	197/88	178/124	-	375	Weltz 2000
New Mex	230	fair	-	-	65/9	16/3	-	78	Weltz 2000

Table 3.4. Fuel loads in North American grasslands-continued.

<i>Mixed grass prairie</i>									
General	-	-	-	-	200-400	-	-	-	Sala 1988
N Dakota	350	ungr	254	293	547	320	613	867	Sims 1978
"	"	graz	220	300	520	66	366	586	
	446	ungr	296/63	200	496	140	340	636	Biondini 1998
"	"	mod	296	200	496	140	340	636	
"	"	hvy	296	1	297	3	4	300	
ND?	441	P prat	-	-	337?	-	-	-	Lura 1992 ***
S Dakota	350	ungr	164	70	234	247	317	481	Sims 1978
"	"	grazed	104	39	143	174	213	317	
Kansas	550	ungr	116	80	196	622	702	818	Sims 1978
"	"	grazed	111	41	152	119	160	271	
Oklahoma	766	ungr	80-90	130	210-220	-	-	-	Gillen 2000
Texas	680	mod	122	96	218	-	-	-	Heitschmidt 1989
"	"	hvy	74	61	134	-	-	-	
	~400	norm	-	-	105	-	-	-	Ralphs 1990
"	"	hvy	-	-	64	-	-	-	

Table 3.4. Fuel loads in North American grasslands-continued.

Tall grass prairie									
General	-	-	-	-	500-600	-	-	-	Sala 1988
Nebr	680	2yPF	281/16	89/9	370	318/19	407	688	Masters 1992
NB?	824	crp1	252	43	295	349	392	644	Schlacht 1998
	"	crp2	815?	28+?	-	580	-	-	
Illinois	-	-	-	-	-	-	[420-1757=852]		Branch 1998
Kansas	814	-	510	-	-	-	742	1252	Hulbert 1988
	814	-	350	150-200	500	800	950	1300	Gibson 1988
	830	noF	238/17	92/10	330	676/38	768	1006	Wessman 1997
	"	10yPF	236/24	24/3	260	743/57	767	1003	
	"	2yPF	281/16	89/9	370	318/19	407	688	
	735	bottom	566	-	-	-	-	-	Piper 1995
	"	poor	232	-	-	-	-	-	
Oklahoma	920	ungr	270	327	597	256	583	853	Sims 1978
	"	graz	340	77	417	424	501	841	
	920	ungr	270	420	690	433	853	1123	Parton 1980
	"	modG	257	435	692	384	819	1076	
	"	3yPF	305	494	799	492	986	1291	
Missouri	937	"	-	-	479/65?	414/54	-	893	Buyanovsky 1987
state	pptn	note	prod	stdd	p+ sd	litter	litt+ sd	fuel	authority

¹ annual precipitation, mm. ² notes refer to species (agsm, bogr, popr) range condition (excell-good-fair), or grazing level (grazed-ungrazed, light-medium-moderate-heavy) or years post-fire. ³ produced in current year. ⁴ dead material produced in current or preceeding years, ⁵ production plus standing dead, ⁶ litter, ⁷ litter plus standing dead, ⁸ fuel= standing live + standing dead + litter, ⁹ published source, often with multiple authors.

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CHAPTER 4

LITTER AND LITTER EFFECTS IN
TALL, MIXED, AND SHORT GRASS PRAIRIES OF THE NORTHERN PLAINSIntroduction

Litter (or mulch) is the aboveground fallen biomass present in an ecosystem (Hulbert 1969; Tomanek 1969). Its hypothetical functions include environmental effects [temperature modification (Facelli & Pickett 1991; Bragg 1995), soil water modification (Ketling 1954; Tomanek 1969; Hulbert 1969), and nutrient reserve (McNaughton 1984; Hulbert 1988; Jaramillo & Detling 1988; Holland & Detling 1990; Holland et al. 1992; Foster 1999)], providing cover for ground dwelling organisms [such as birds (Bragg 1995; Knopf 1996), mammals (Tomanek 1969; Kaufman et al. 1990; Bragg 1995; Benedict et al. 1996), insects (Bragg 1995; Whelan 1995; Arenz & Joern 1996)], and microbes (Holland & Detling 1990; Holland et al. 1992)], favoring plants with apical growth (forbs) over those with basal meristems (grasses, Penfound 1964; Dahl & Hyder 1977; Grime 1979; Whelan 1995), and providing fuel for prairie fire (Tomanek 1969).

Litter dynamics determine litter loads and their influences in grasslands of the Great Plains. After a fire litter gradually accumulates in tall (Knapp & Seastedt 1986; Ewing & Engle 1988), mixed (Dix 1960; Redman et al. 1993), and short grass prairies (Jaramillo & Detling 1988). Litter loads tend to increase for 4-5 years until they reach an equilibrium where decomposition equals accumulation rate (Dix 1960; Redman et al. 1993; Erichsen-Arychuk et al. 2002). Nitrogen bound in heavy loads probably limits forage production in tall, mixed, and short grass systems (Schimel et al. 1985; Hulbert 1988; Hobbs & Huenneke 1992; Groffman et al. 1993). One also expects phosphorus limitation, but this effect has not been documented (Schimel et al. 1985; Hobbs & Huenneke 1992; Burke & Grime 1996; Buckland et al. 2001).

Our work compares litter dynamics, quantities, qualities, and effects across major grassland types of the northern plains as a basis for understanding litter impact in these systems. Specifically, we ask: 1) How do litter loads (g/m^2) increase after fire? 2) How do equilibrium loads (gm/m^2) differ among major grassland types? 3) What are the carbon and nitrogen contents of equilibrium loads? 4) What are the carbon and nitrogen release rates from equilibrium loads? 5) How do litter loads affect soil temperature and water? 6)

Does litter affect forage production or composition? Our comparisons are well controlled because studies were made on sites in the hill and pothole topography of the Missouri Coteau (the terminal moraine of the continental glacier, Pielou 1991) where micro environmental differences support adjacent stands of tallgrass (bottoms, *Andropogon gerardi*), mixed grass (slopes, *Schizachyrium scoparium*), and shortgrass (*Boutaloua gracilis*).

Methods

We compare litter and litter processes in tall, mixed, and short grass prairie sites which are burned/unburned and clipped/unclipped(grazed/ungrazed). We do so by interpreting a three level management experiment design in which areas with different fire treatments (8) include blocks with major grassland types (3) within which 2-3 clipping treatments were applied, for a total of 72 sites.

The geological and fire history of the Lostwood NWR makes it a perfect location for this study. 1) Its well recorded fire history provides units unburned for one to over fifty years. 2) Its rolling morainial topography provides sites within fire treatments which occupy bottoms (relatively moist), slopes, and ridges (relatively dry) which are occupied by vegetation similar to tall, mixed, and short grass prairies of the Great Plains respectively. 3) Within each of these twenty-seven sites we installed three 3x4m clipping plots (simulated grazing plots). These lay side-by-side on a contour line, but separated by 1meter strips. One was unclipped (standing crop and litter intact), one was clipped (standing crop removed), and one was clipped and raked (standing crop and litter removed by brisk raking). The clipping treatments were randomly assigned to the plots.

End-of-season standing crop was measured on each 3x4m plot (eight slopes x 3 topographic positions x 3 clipping treatments) by clipping two 30x60 plots, separating (grass, forb, and shrubs), drying, weighing, and expressing as g/m^2 . The data presented here are the average of 1998, 1999, and 2000 harvests.

Over-wintering standing crop was removed from the experimentally treated plots in the springs of 1998, 1999, and 2000. One experimental plot was randomly chosen to be clipped and raked (heavily grazed treatment). A second plot was randomly chosen as the clip only treatment (moderately grazed). The third

plot was left undisturbed. Standing crop was cut to 5 cm with a weed whip and gathered carefully with a broom rake so as not to disturb the litter. In 1999 the harvest was weighed wet, sampled (10%), and converted to dry weight by multiplying by the sample's dry weight/wet weight ratio.

While these treatments attempt to simulate the effects of grazing on litter (Weaver & Hougen 1939; Dix 1960; Penfound 1964; Smoliak et al. 1971), it does not mimic other affects of grazing such as herbivore selectivity and repetitive consumption (Stoddard & Smith 1943; Smoliak et al. 1971; Noy-Meir 1978; McNaughton 1979, 1986; Biondini & Manske 1996). Litter was removed from the heavily grazed plot in spring 1998, 1999, and 2000 after the standing dead was removed. This involved vigorous and repeated raking with a broom rake. In 2000 the harvest was weighed wet, sampled (10%), and converted to dry weight by multiplying by the sample's dry weight/wet weight ration. The dry litter sample still contained soil. This was removed by grinding 25% of the litter sample, then ashing the sample at 550C for six hours and multiplying the dry weight by (sample weight- ash weight)/sample weight ratio.

Carbon and nitrogen contents of the forage, standing dead, and litter were measured to observe the effects of environmental (topography), seral stage (time-since-fire), and grazing (litter management) on it. A sample (100% of the forage, 25% of the standing dead, and 25% of the litter sample) was ground and thoroughly mixed. The MSU soil testing lab measured carbon and nitrogen with a LECO analyzer (Bremner 1996; Nelson and Sommers 1996).

Litter dynamics were estimated by graphing litter weight against time (Fig. 4.1). Accumulation rates on the tall, mixed, and shortgrass curves (Fig. 4.1) were estimated with regressions (Table 4.1). On the rising (0-4 years) and equilibrium (5-50 years) arms of the biomass over time curve. The equilibrium litter load was estimated as the average of weights after the curve leveled. N delivery after equilibrium is assumed to equal the rate of pre-equilibrium litter accumulation x % nitrogen. This follows from the fact that production is similar pre- and post-equilibrium, that the cessation of accumulation implies that production equals decomposition, and that nitrogen in the 'missing accumulation' is being released by decomposers.

Litter effects on the soil environment were estimated by measurements on littered and de-littered plots. 1) Temperature effects were measured by comparing soil temperatures (15 cm depth) measured in adjacent plots with thermocouples (Taylor & Jackson 1986). 2) Soil water effects were compared by measuring soil water (15 cm) on adjacent plots with plaster blocks (Gardner 1986) at 15cm. Both comparisons were made by plotting the temperature difference for each pair of plots against time (Kleinbaum et al. 1988; SPSS, Inc. 2000) finding the difference, and testing season long with a paired t-test (Kleinbaum et al. 1988; SPSS, Inc. 2000).

Litter effects on plant performance were measured by comparing production on littered plots and plots de-littered in 1998, 1999, and 2000. We believe the effects of mechanical de-littering on litter bulk (eg. on light, temperature, moisture, and nitrogen) are similar to those of fire or grazing (Aldous 1930; Penfound 1964; Hulbert 1988; Willms et al 1993).

Environmental changes on the topographic and vegetational gradients expected from vegetational differences were verified with field sampling similar to that comparing litter effects above. The MSU soil testing lab measured carbon, nitrogen, pH, and conductivity (salinity) of soil samples from each site as indicators of soil nutrients/toxicity. Carbon and Nitrogen were measured with the LECO CNS (Nelson & Summers 1996; Bremner 1996). Conductivity and pH were measured on 1:1 soil water slurries with appropriate meters (Thomas & Rhoades 1996). Soil texture was measured with the Boyoucos hydrometer method (Gee & Bauder 1986).

Results and Discussion

Litter accumulates for three to five years after a fire event and levels off in tall grass and mixed grass prairie of the Couteau (Fig 3.1). Accumulation persists for many years in the shortgrass environment (Fig 3.1), perhaps because the environment is too dry for decomposers. While rapid accumulation and early equilibrium have also been observed in tall (Dahman & Kucera 1965) and mixed grass prairie of the plains (Redman et al. 1993), we have no corresponding reports for long term accumulation in short grass prairie.

Equilibrium litter loads are estimated as 330 g/m^2 , 310 g/m^2 , and 148 g/m^2 in tall, mixed, and short grass prairie (Fig 4.1, Table 4.1). The size of the equilibrium load is a product of essentially constant inputs balanced against losses that increase with time and load (presumably because longer humid periods associated with a thick litter layer favor decomposers). The higher loads of tall and mixed grass vegetation are associated with their higher production and appear in spite of the relatively high decomposition rates expected in their moister microenvironments. The continuing rise in the shortgrass litter load raises the possibility that it might exceed the tallgrass litter load; if so, this may be due to extreme reduction of decomposition rate on the dry sites.

Carbon and nitrogen contents of Coteau litter don't vary with either age or vegetation type (Table 4.5). Carbon contents are $43 \pm 1.3(\text{se})$, $42.4 \pm 1.9(\text{se})$, and $41.0 \pm 1.2(\text{se})$ percent of tall grass, mixed grass, and short grass vegetation. Corresponding nitrogen contents are $1.14 \pm 0.1(\text{se})$, $1.36 \pm 0.1(\text{se})$, and $1.32 \pm 0.0(\text{se})$ percent. Decomposing litter presumably releases most of its carbon to the atmosphere and most of its nitrogen to the soil (McNaughton et al. 1982; Parton & Risser 1980; Bazzaz 1996). While burning is expected to release both carbon and nitrogen to the atmosphere, significant amounts may be retained in the system (Koelling & Kucera 1965).

Delivery of nitrogen from litter to soil is quasi-constant (with weather driven fluctuation) in the equilibrium system. Delivery rates are approximated by pre-equilibrium accumulation, because net accumulation ceases at equilibrium and quantities of litter corresponding to pre-equilibrium accumulation must be released to balance income. Thus nitrogen delivery rates are approximately $0.77 \text{ g/m}^2/\text{yr}$, $0.86 \text{ g/m}^2/\text{yr}$, and $0.40 \text{ g/m}^2/\text{yr}$ for tall grass, mixed grass, and short grass prairie. These figures may be minimal because some delivery (eg leaching of nitrogen) may occur before significant weight loss occurs. The bottom and mid slope sites have C/N higher ratios (41.76 & 34.56) while the hill top sites have a lower ratio (32.82, Table 4.7). This indicates a higher decomposition rate on the two lower sites which are offset by the increased production of these sites (Table 4.1).

Soil temperature at 15 cm in de-littered plots was lower in spring, became warmer in mid-summer, and stayed warmer in late fall relative to littered plots (control or unburned) (Table 4.4, Fig 4.2). Over the complete growing season de-littered plot soils (15cm) were very different, sometimes cooler and sometimes

warmer. Spring warming and fall cooling were retarded in littered plots probably because the litter reduced convective exchanges. The differences in temperature are attributed entirely to differences in litter loads, because standing crops, the other likely factor, did not differ between the litter treatments (Table 4.2).

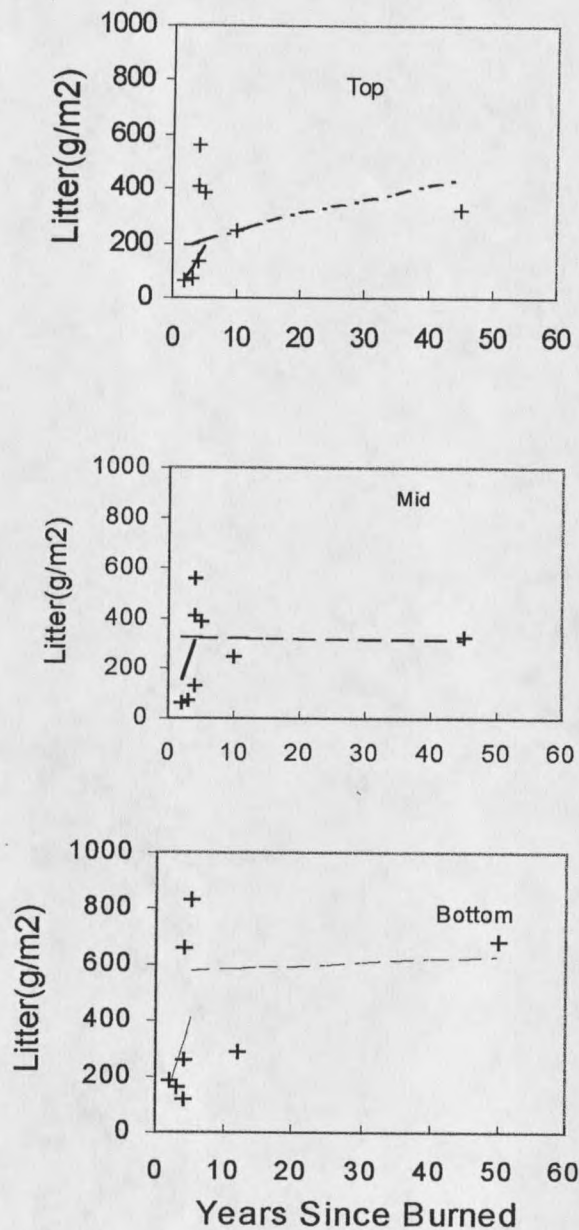


Figure 4.1. Accumulation of litter in tall(bottom), mixed(slope), and short(top) grass prairies through fifty years against time since the site was last burned. Regression through 1-4 years (left column) and 5-50 years data (right column) plotted with actual data point. Regressions are in Table 4.1.

Table 4.1. Litter loads (g/m^2) and accumulation rates ($\text{g/m}^2/\text{yr}$) predicted in three grasslands: tallgrass(bottom), mixed grass (slope), and shortgrass (top). The first regression is calculated by regressing all data points within the strata. The second regression (1-4 yrs) runs through the origin and 1-4 year data. The third regression line in each stratum runs through data recorded 5-50 years since last burned.

BOTTOM:

TIME	MODEL	R2	P VALUE	MAX	MEAN
1-50yrs	$L=328+7.1*\text{YRS}$	0.17	$P=0.30$	827	398 ± 278
1-4 yrs	$L=82.4*\text{yrs}$	0.71	$P=0.03$	660	278 ± 220
5-50yrs	$L=571+1.2*\text{YRS}$	0.01	$P=0.93$	827	598 ± 278

Using the regression for 1-4 years to predict the amount of litter after 4years= 329.6 g/m^2

MID SLOPE:

TIME	MODEL	R2	P VALUE	MAX	MEAN
1-50yrs	$L=258+2.17*\text{YRS}$	0.02	$P=0.73$	558	274 ± 178
1-4 yrs	$L=77.6 * \text{yrs}$	0.73	$P=0.03$	558	246 ± 224
5-50yrs	$L=326-0.24*\text{YRS}$	0.01	$P=0.94$	325	286 ± 55

Using the regression for 1-4years to predict the amount of litter after 4years= $310.4/\text{m}^2$

TOP OF HILL:

TIME	MODEL	R2	P VALUE	MAX	MEAN
1-50yrs	$L=117\pm6.6*\text{YRS}$	0.58	$P=0.03$	420	186 ± 141
1-4 yrs	$L=37.1*\text{yrs}$	0.74	$P=0.03$	271	121 ± 100
5-50yrs	$L=185+5.1*\text{YRS}$	0.69	$P=0.37$	420	295 ± 144

Using the regression for 1-4years to predict the amount of litter after 4years= $148.2/\text{m}^2$

1. Litter estimations at equilibrium at 4 years on bottom, mid slope, and hilltop topographic positions using the 1-4 year regression at each topo level.

Soil water availability at 15 cm differed little between littered and de-littered plots (paired t-test, $t=1.81$ with 464 df, $p=0.071$), regardless of season. Thus spring water contents were similar (Fig 4.2), presumably because all soils were wet by pre-season snow and rain. Early summer soil water did not differ between the plots (Fig 4.2), probably because litter did not significantly reduce evaporation. Late summer soil water was not affected (Fig 4.2), likely because litter did not intercept enough water to reduce supplies to the 15 cm level. The differences in soil water are attributed entirely to differences in litter loads, because standing crops, the other likely factor, did not differ between the litter treatments (Table 4.3).

Table 4.2. End of season standing crop in tallgrass(bottom), mixed grass(slope) and short grass (top) sites. 1998-2000 data averaged.

	Bottom	Slope	Top	p-value
Total(g/m ²) ¹	268±84(sd)	207±71(sd)	141±44(sd)	p<0.001, F=2.82, 19df

1. End of season standing crop values are least squared means.

Accumulation of litter is hypothesized to reduce production, through reduction of temperature, water, nutrient, and/or light for plants with basal meristems (grasses). On our paired experimental plots we saw no such reduction after three years of treatment (Table 4.3). We cannot exclude the possibility that longer treatment might reduce growth, since litter loads (and their effects) continue to increase through the 5-10th year (Fig 4.1).

Table 4.3. Effect of simulated grazing on end of season standing crop. Data averaged of 1998-2000.

	Heavy grazed ²	Light grazed ²	Ungrazed ²	p-value
Total(g/m ²) ¹	199±9.5(sd)	200±31(sd)	219±9.4(sd)	p=0.411, F=0.89, 254df

1. End of season standing crop values are least squared means.

2. Simulated grazing in spring removed litter and standing crop (heavy), standing crop only (light), or neither (ungrazed).

Table 4.4. Soil temperature regression. Soil temperature(15cm depth) regressed against season day, topographic position, simulated grazing treatment, water, and the interaction of these factors as predictors.

	Coefficient	P-level
CONSTANT	-47.10958	>0.001
Julian day	0.64965	>0.001
Julian day*Julian day	-0.00163	>0.001
Topo position	0.81057	>0.001
Day*Treatment	-0.00203	>0.001
Water	-0.13139	0.0003
Adjusted squared multiple R: 0.714		

Table 4.5. Litter composition (carbon and nitrogen) by topographic position.

Position	Bottom	Slope	Top	P-value
Carbon(%)	43.1 $\pm$ 1.1A	42.4 $\pm$ 1.1A	41.0 $\pm$ 1.1 A	p=0.069, F=3.01, 23df
Total Carbon ¹	134.0 $\pm$ 19.C	77.6 $\pm$ 19.8 B	59.6 $\pm$ 19.8A	p=0.001, F=29.06, 49df
Nitrogen(%)	1.14 $\pm$ 0.08A	1.36 $\pm$ 0.0 A	1.32 $\pm$ 0.08A	p=0.142, F=2.12, 23df
Total Nitrogen ¹	3.59 $\pm$ 0.2 C	2.67 $\pm$ 0.2 B	1.70 $\pm$ 0.2A	p=0.001, F=18.3, 49df
C/N Ration	41.8 $\pm$ 2.4 B	34.6 $\pm$ 2.4 A	32.8 $\pm$ 2.4 A	p=0.020, F=4.15, 49df

1. Totals (nitrogen and carbon) are calculated by multiplying the % content (C or N) times the total amount of litter produced at each topographic position (values are g/m²). The values are least squared means.

Table 4.6. C/N ratios of litter on recently burned and long unburned sites.

Years/burned	1-3yrs	4-5yrs	6-10yrs	10-50yr	P-value
C/N ratio ¹	45.1 $\pm$ 4.8A	35.8 $\pm$ 4.8A	34.6 $\pm$ 2.5A	32.6 $\pm$ 2.8A	0.19, F=1.72, 22DF

1. Values are least squared means with letters representing significance at p=0.05 level.

Litter is the fallen standing crop of previous growing seasons. The carbon content of end-of-season standing crop is 2-3% higher than that of litter (Tables 4.5 & 4.7). Nitrogen contents are similar. C/N ratios were not significantly different between litter and end-of-season standing crop (paired t-test, $t=0.676$, $p=0.507$). These data supports the hypothesis that little carbon and nitrogen is lost from standing dead over the winter on our sites. Other authors found significant losses in the standing crop component before it becomes litter for selected species (Koelling & Kucera 1965; Buyanovsky et al 1987).

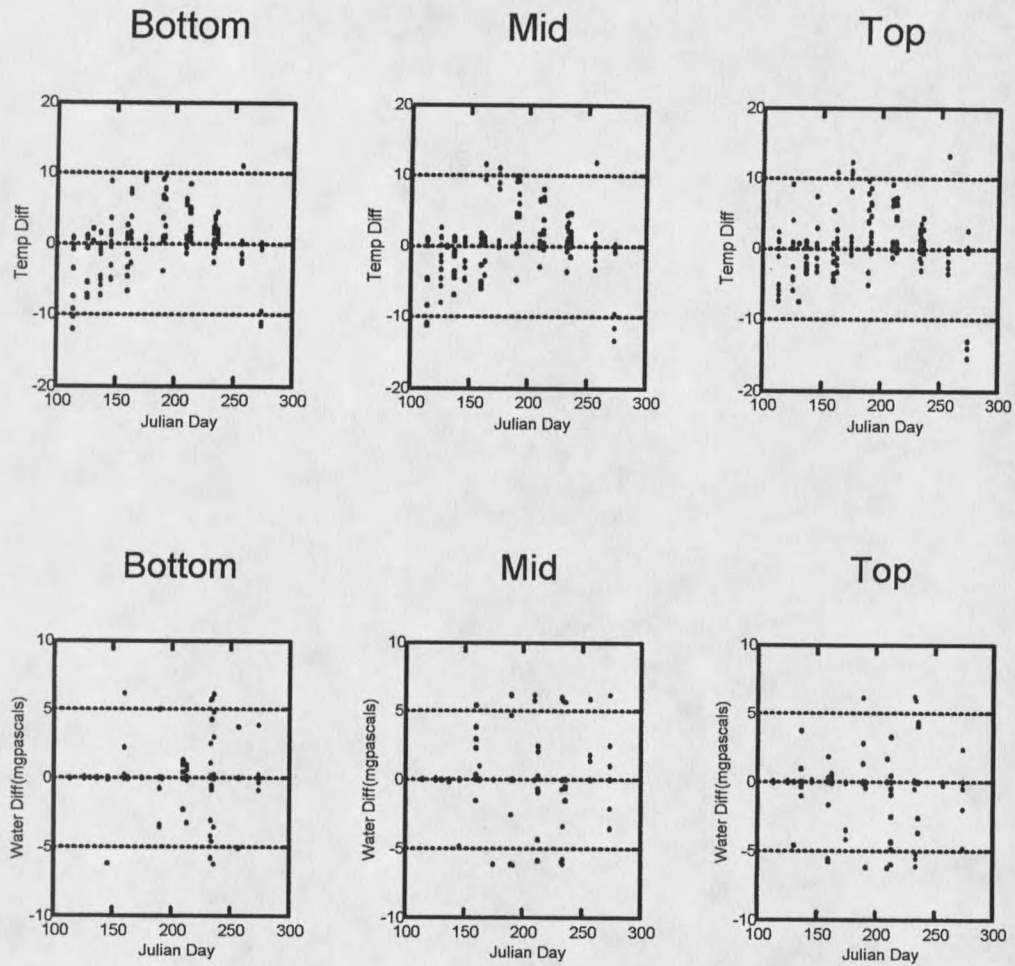


Fig. 4.2. Cross-season comparison of soil temperature(C) and soil water on littered and de-littered plots (the difference was found by subtracting the littered plot from the de-littered observations) against the growing season (measured by Julian Day).

Table 4.7. Nitrogen and carbon content of end of season standing crop.

BOTTOM	Litter Free	Littered	(LF-Littered)	Number
Carbon(%)				
1-3yrs	45.90	44.90	1.00	1
3-10yrs	45.32	45.40	-0.08	5
10-50yrs	46.03	45.77	0.26	3
Nitrogen(%)				
1-3yrs	1.17	1.33	-0.16	1
3-10yrs	1.21	1.21	-0.01	5
10-50yrs	1.32	1.26	0.06	3
Carbon/Nitrogen Ratio				
1-3yrs	39.23	33.76	5.47	1
3-10yrs	37.84	38.49	-0.95	5
10-50yrs	35.00	36.36	-1.36	3
MID SLOPE	Litter Free	Littered	(LF-Littered)	Number
Carbon(%)				
1-3yrs	45.50	45.70	-0.20	1
3-10yrs	45.50	45.24	0.26	5
10-50yrs	46.33	46.03	0.30	3
Nitrogen(%)				
1-3yrs	1.50	1.46	0.04	1
3-10yrs	1.38	1.29	0.09	5
10-50yrs	1.46	1.43	0.03	3
Carbon/Nitrogen Ratio				
1-3yrs	30.33	31.30	-0.97	1
3-10yrs	33.46	35.41	-1.95	5
10-50yrs	31.94	32.90	-0.96	3
HILL TOP	Litter Free	Littered	(LF-Littered)	Number
Carbon(%)				
1-3yrs	44.70	45.40	-0.70	1
3-10yrs	45.83	45.85	-0.02	5
10-50yrs	45.80	45.57	0.23	3
Nitrogen(%)				
1-3yrs	1.43	1.18	0.25	1
3-10yrs	1.30	1.26	0.04	5
10-50yrs	1.55	1.45	0.10	3
Carbon/Nitrogen Ratio				
1-3yrs	31.26	38.47	-7.21	1
3-10yrs	35.73	36.80	-1.07	5
10-50yrs	29.74	31.45	-1.71	3
Probabilities	Carbon	Nitrogen	C/N Ratio	
Topo	p=0.818, F=0.20,42df	0.001, F=5.66,42df	p=0.010, F=5.09,42df	
Treatments	p=0.468, F=0.54,42df	0.210, F=1.66,42df	p=0.240, F=1.37,42df	
Burn time	p=0.304, F=1.22,42df	0.001, F=3.24,42df	p=0.010, F=2.88,42df	

Note: We found no significant interactions between the previous factors.

Our simulated grazing did not change the standing crop quality. Nitrogen content of forage did not vary among treatments in our grazing experiment (Table 4.7). Other papers report that nitrogen content was higher on ranges grazed than on ungrazed sites (McNaughton 1979; Risser & Parton 1982; Holland & Detling 1990; Holland et al. 1992; Dyer et al. 1993; Biondini et al. 1998).

On the other hand, fire history did change the standing crop quality with higher nitrogen content on sites unburned for longer periods (Table 4.7). Carbon content was unaffected by burn history (Table 4.7). The net result is a lower C/N ratio in end of season standing crop in older stands.

Conclusion

In conclusion, litter amounts are highest in tallgrass which results in higher carbon and nitrogen on these sites. Decomposition rates are higher on tallgrass sites also. High production results in litter accumulation until it reaches an equilibrium level after 4-5 years. Mid slopes are similar to bottom sites with slightly lower rates of production and litter accumulation. Ridgetops have still lower rates of accumulation which slows after 4-5 years, but does not reach an equilibrium for at least 50 years. Carbon and nitrogen content of both litter and end-of-season standing crop are similar to each other as well as the content of standing crop and litter on different topographic levels (Tables 4.5 & 4.7). Burning history did affect the quality of standing crop (Table 4.7) with higher levels of nitrogen in stands that remained unburned for longer periods.

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CHAPTER 5

VEGETATION TYPE CONVERSION:
MIXED GRASS PRAIRIE TO CLONAL WEEDSIntroduction

'Type conversion' occurs when the vegetation occupying a site is replaced by another type. Examples are diverse. An early seral stage may be replaced by a later stage (Odum 1969; Burrows 1990). A suppressed component species may become more dominant when a limiting factor is removed (eg. woody plants in grasslands when fire is excluded, Axelrod 1985; Anderson 1990; Collins & Gibson 1990; Collins & Wallace 1990; Archer 1994). A species from a similar environment may invade if disturbance facilitates its establishment (eg. grazing, Milchunas et al. 1988; Hobbs & Huenneke 1992)) or if an excluding force (eg. fire, Hobbs & Huenneke 1992) is removed. An exotic species may invade if it finds a niche and may dominate if it is very competitive. Man may establish a crop by removing existing vegetation and inserting the alternate.

A type conversion may be viewed as good or bad by different characters . For example, change in species composition, diversity, structure, production will affect habitat for one associate differently from others (eg. subordinate plants, invertebrates, birds, and mammals) and quality/quantity of economic yields (eg. forage to lumber).

While changes are sought or fought by those with different goals, alternate ecosystems are rarely compared systematically. Parameters for such comparison might include composition and standing crop, structure (vegetation stratification), function (phenology and productivity), and environmental effects. Odum (1969) compared seral stages. Buyanovsky et al. (1987) compared wheat and tall grass prairie. It is our object to compare three alternate vegetation types commonly occupying the mixed grass environment of the central plains: native grass, exotic *Bromus inermis*, and *Symphoricarpos occidentalis*. The native grass of the central prairies (Coupland 1950, 1961) is dominated by the Stipa- Bouteloua association. *Bromus inermis* (smooth brome), a pasture grass from Russia, is colonizing and dominating large areas of mixed

grass prairie (Bragg & Steuter 1996). With fire suppression, native shrubs of the mixed grass prairie (eg *Symphoricarpos* spp), are expanding to dominate mixed grass environments.

Grasslands have been characterized as being stable and difficult for alien species such as *Bromus inermis* to invade (Weaver 1934, 1954; Coupland 1950). It has been suggested that it is easier for alien species to invade areas that have a low species diversity (Tilman 1997; Stohlgren et al 1998; Stohlgren et al 1999; Foster 2000) and along environmental gradients with more moisture and higher fertility which may produce higher amounts of standing crop (Tilman 1988; Stohlgren et al 1998; Bonser & Reader 1995; Foster 2000). Under this hypothesis alien plants would be more likely to successfully invade sites in grasslands next to water sources such as prairie pothole ponds where water is more available (Knapp et al. 1993; Peltzer et al. 1998). Ridgetops should be less invadable under this hypothesis. Soil disturbance such as rodent activity (larger rodents may create larger disturbances than other), periodic fires, and grazing which create openings in the established vegetation for resources may be necessary for many plant species to successfully invade an existing prairie plant community (Sousa 1984; Platt & Weis 1977; Hobbs & Huenneke 1992).

Methods

Our studies were conducted on the Lostwood National Wildlife Refuge, Kenmare, North Dakota which lies on the Missouri Coteau, the terminal moraine of the continental glacier (Pielou 1991, 1998). The moraine provides a rolling topography in which ponds occupy low sites and ridges intervene. Tall grass vegetation occupies bottoms, slopes are covered with mid-grass, and shortgrass covers hilltops. The macroclimate of Lostwood NWR is continental with cold winters and hot summers (Weaver 1980). Average rainfall between 1936 and 1989 averaged 419 mm (309mm-497mm) (Kruse & Bowen 1996) with most falling in May-June (Coupland 1950, 1961; Weaver 1980).

To compare the performance of mixed grass, *Bromus*, and *Symphoricarpus* in the mixed grass environment, we sampled mixed grass vegetation and embedded brome and snowberry clones. To simultaneously examine the effects of time since fire we chose blocks representing recently burned sites (1-2 years) to sites unburned for over 50 years (Table 5.1). At each site we staked three 3x4m plots on the mid slope between the pothole pondside vegetation and the adjacent ridgetop. The first plot was staked within

the invader sparse native vegetation. A second plot was staked within a clone of *Bromus inermis*. A third 3x4 m plot was staked in a *Symphoricarpus occidentalis* clone as close as possible to the native plot. Plots in a block were all placed on the same contour and were less than 25 meters apart.

The validity of comparing the effects of dominant communities in this way depends on their occupying a uniform environment. The macro-environment at each of the 8 replications was identical because the mixed grass prairie and invader colonies occupied adjacent parts (less than 25 meters apart) of the same site. Identity of the micro-environments was assumed to be well mixed; this was tested by comparing the texture of soils from the surface horizon (10cm) in each community. The soils were sampled with twenty 2.5 cm cores. Texture was measured by the Boyoucos method (Gee & Bauder 1986).

The species composition of the mixed grass, *Bromus*, and *Symphoricarpus* communities were compared by listing species present in each community at each of the eight sites. Species present were listed once and the list enlarged with observations on seven successive visits (dates listed below with reflectance dates). Species nomenclature follows those of the Great Plains Flora Association (1991).

End-of-season forage was sampled as an index of production. The mass of each standing crop component (grass, forb, and shrub) in mixed grass, snowberry, and brome plots was compared by sampling on eight sites with an August harvest (1998, 1999, and 2000). Material was harvested on two 1x2 (30 x 60 cm) foot plots in each community type. Current years forage was clipped, dried, weighed, and these data were scaled up to g/m^2 .

As an index of phenology (chlorophyll mass) we measured reflectance periodically at each of the 24 sub-sites (three plots on eight sites) throughout the seasons of 1998, 1999, and 2000. 1) Eight, eight, and two dates were sampled respectively in 1998 (April 17-24, May 18-25, June 10-13, June 23-27, July 9-12, July 27-30, August 20-26, & September 12-15), 1999 (April 23-26, May 9-12, May 26-29, June 12-17, July 7-13, July 30-August 3, August 22-27, & Oct 30-Nov 3), and 2000 (May 3-7 & June 3-7). 2) Measurements were made with a 'Cropscan differential radiometer' which compares incoming radiation with reflected radiation in the blue (485 nm), green (560 nm), red (660 nm), near infrared (830 nm) and infrared (1650 nm) bands (Aase et al. 1987; Goodin & Henebry 1997). These wavebands are sufficiently similar to Landsat wavebands to allow extrapolation of our results to Landsat imagery. We also tested NDVI

(normalized difference vegetation index, (NIR-Red)/(NIR+ Red) (Wessman et al 1997; Davidson & Csillag 2001), since it is commonly used as an index of biomass. 3) The usual precautions were taken to avoid biasing reflectance data. To minimize sun angle effects, measurements were made at mid-morning (9:00-11:00am) and mid-afternoon (1:30-5:00pm) only (Goodin & Henebry 1997). Measurements were not made on excessively cloudy days. Time of measurement was rotated among plots to remove variation associated with the time of measurement (day, reflectance variation). We tested this effect (time of day) on reflectance against time of day by plotting reflectance in all five color bands against time of day (Neter et al. 1990). We could not see an apparent time of day trend in the plots.

We compared soil water, soil temperature, and other soil characteristics under the three communities to test for effects of type conversion on soils. 1) Soil water was measured periodically over three years using plaster blocks buried at 15cm. Conductivity measure with an ohm-meter was calibrated against soils with known water contents (Campbell & Gee 1986). 2) Soil temperature was measured simultaneously with thermocouples buried at 15cm and a micro-volt meter (Taylor & Jackson 1986). The MSU soil testing lab measured carbon, nitrogen, pH, and conductivity (salinity) of soil samples from each site as indicators of soil nutrients/toxicity. Carbon and Nitrogen were measured with the LECO CNS (Nelson & Summers 1996; Bremner 1996). Conductivity and pH were measured on 1:1 soil water slurries with appropriate meters (Thomas & Rhoades 1996). Soil texture was measured with the Boyoucos hydrometer method (Gee & Bauder 1986).

Systat (SPSS, Inc 2000) was used to make our statistical analysis which included multiple regressions and ANOVA in our analysis.

Results

Type conversion reduced the richness of mixed grass ecosystems, with numbers of common species (constancy >70%) being eight in mixed grass, two in brome, and three in snowberry (Table 5.1). Clonal invaders (*Poa*, *Bromus*, and *Symphoricarpos*) were present in all three types. Most native species are present, at least occasionally in all three types.

Table 5.1. Species list by type of plot at mid slope. Species occurring at two or more sites are listed. Data is entered as the percentage (%) of the sites in which the species were present.

Species Name	native ¹	snowberry ¹	bome ¹
GRASSES			
<i>Stipa comata</i>	91	27	18
<i>Agropyron smithii</i>	9	9	
<i>Poa pratensis</i>	100	91	55
<i>Bromus inermis</i>	91	36	100
<i>Schizachyrium scoparium</i>	36		9
<i>Andropogon gerardi</i>	9		
<i>Spartina pectinata</i>	9		
FORBS			
<i>Potentilla argula</i>	18		
<i>Echinacea pallida</i>	27		27
<i>Artemisia frigida</i>	55	9	27
<i>Anemone patens</i>	55	18	36
<i>Achillea millefolium</i>	73	64	45
<i>Psoralea tenuiflora</i>	18	9	9
<i>Helianthus annuus</i>	36		9
<i>Artemisia ludoviciana</i>	55	36	27
<i>Astragalus crassiocarpa</i>	18	9	
<i>Cerastium arvense</i>	18	9	9
<i>Sphaeralcea coccinea</i>	55	27	
<i>Solidago speciosa</i>	91	45	9
<i>Galium boreale</i>	100	55	36
<i>Liatris aspera</i>	27		9
<i>Campanula rotundifolia</i>	36	18	
<i>Topogon dubius</i>		27	27
<i>Vicia Americana</i>	27	18	27
<i>Astragalus Canadensis</i>	9	18	36
SHRUBS			
<i>Rosa woodsii</i>	91	73	36
<i>Elaeagnus comuntata</i>	45	9	9
<i>Symphoricarpus occidentalis</i>	100	91	73
Richness			
Constancy>75%	8	2	1
Constancy>50	12	5	3
Constancy>25	19	11	13

¹ Native describes mid slope plots that have not been invaded by snowberry or brome. Snowberry are plots dominated by *Symphoricarpus occidentalis*. Brome are plots dominated by clones of *Bromus inermis*.

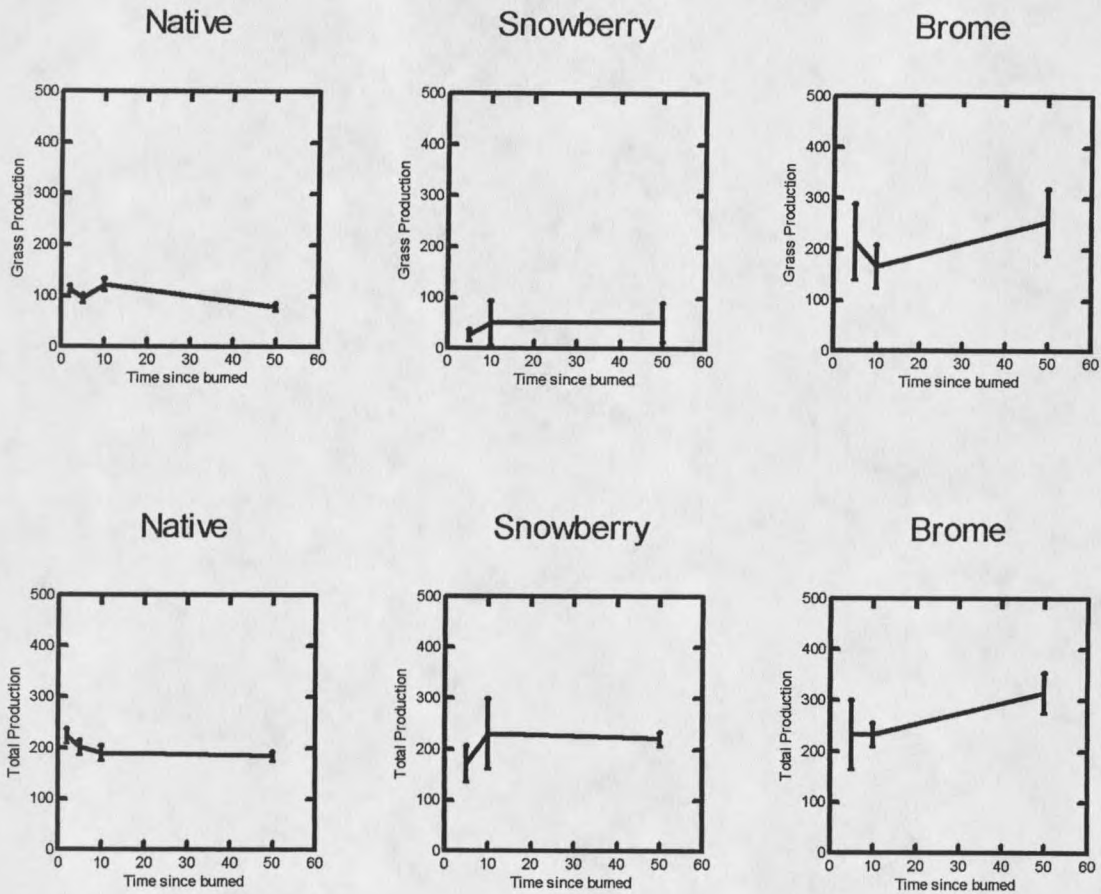


Fig 5.1. End of season standing crop by component. The Y axis are labeled by component measured in grams/ meter squared. The X-axis is measured in years since the site was last burned. Native stands are the mid slopes which appear to represent the majority of mid slope vegetation. Snowberry designates the sites that are dominated by *Symphoricarpus occidentalis*. Brome sites are dominated by *Bromus inermis*. Error bars represent standard errors from the mean.

Table 5.2. Forage production (g/m^2)(end-of-season standing crop) in mixed grass, snowberry, and brome vegetation. Neither wood nor root production is included.

	STANDING CROP(End of Season)			
	native ¹	sno ¹	brome ¹	p value
Total ²	$199 \pm 7.8\text{A}$	$204 \pm 21.0\text{A}$	$259 \pm 20.1\text{B}$	0.002, F=6.53, 113df
Grass ²	$101 \pm 7.0\text{B}$	$41 \pm 19.1\text{A}$	$210 \pm 19.0\text{C}$	<0.001, F=31.64, 113df
Forb ²	$56 \pm 3.6\text{C}$	$23 \pm 9.8\text{B}$	$1 \pm 9.8\text{A}$	<0.001, F=14.27, 113df
Shrub ²	$42 \pm 6.3\text{A}$	$140 \pm 17.0\text{B}$	$48 \pm 17.0\text{A}$	<0.001, F=17.52, 113df

1. Types are defined as one of five vegetation types(native= native grass sites on mid slopes sites between the bottoms and ridgetops, sno=snowberry clones, & brome=smooth brome clones.
2. Standing crop means clipped in mid August measured in grams/meters². Means followed by different letters are significantly different at the p=0.05 level.

Forage production increased from native ($199 \pm 7.8 \text{ g/m}^2$) to snowberry ($204 \pm 21.0 \text{ g/m}^2$) to brome ($259 \pm 21.0 \text{ g/m}^2$) (Table 5.1, Fig. 5.1). Because our measure omitted increases in stem thickness, total aboveground production in snowberry may exceed that in brome. Root production was not measured. Forb production was reduced by conversion of mixed grass ($56 \pm 3.6 \text{ g/m}^2$) to snowberry ($23 \pm 9.8 \text{ g/m}^2$), and more so to brome ($1 \pm 9.8 \text{ g/m}^2$, Table 5.2). Grass production was reduced by conversion of mixed grass ($101 \pm 7.0 \text{ g/m}^2$) to snowberry ($41 \pm 19.1 \text{ g/m}^2$), but increased by to brome ($210 \pm 19.1 \text{ g/m}^2$). Shrub production was higher in snowberry ($140 \pm 17.0 \text{ g/m}^2$) than either mixed grass ($42 \pm 6.3 \text{ g/m}^2$) or brome ($48 \pm 17.0 \text{ g/m}^2$). Total forage production (end-of-season standing crop) varied little between recently burned and long unburned stands (Fig 5.1.). Forage production did not include addition to stems of shrubs or addition to roots.

Forage quality, as indexed by nitrogen (protein) content, varied significantly among the vegetation types (Table 5.6). Nitrogen content of brome vegetation (1.008 %) was significantly lower than native (1.30%) or snowberry vegetation(1.24%). This indicates that Brome is lower in protein content on material harvested in August. Many grasses are higher in protein content in early spring and lose much of the proteins as they mature in late summer (Wambolt et al. 1997).

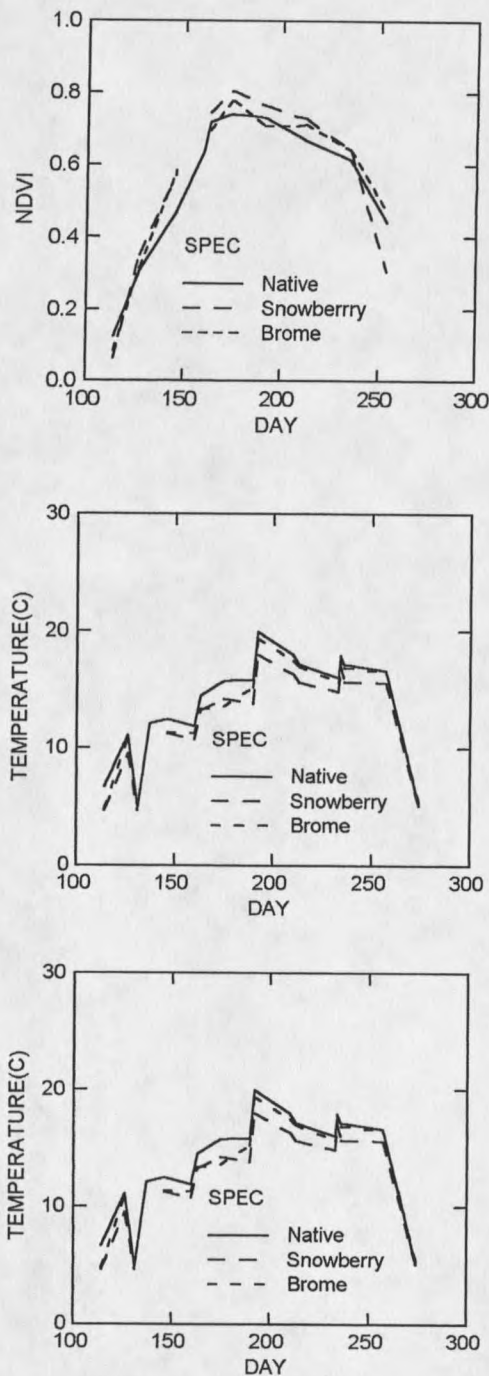


Fig. 5.2. Mid slope soil water, soil temperature, and plant phenology (as measured by NDVI). Native stands are the mid slopes which appear to represent the majority of mid slope vegetation(mean=solid line). Snowberry designates the sites that are dominated by Western Snowberry(mean=long dashed line). Brome sites are dominated by Smooth Brome(mean=short dashed line). Day of season was measured in Julian day of year.

Shrubs such as snowberry remain higher in protein content as they mature (Stoddard & Smith 1943; Plummer et al. 1968). The reduced amount of nitrogen also significantly increases the carbon/nitrogen ratio of Brome vegetation compared to Snowberry and native plot vegetation (Table 5.6).

The phenologies of the three cover types, as indicated by reflectances (NDVI), are nearly identical. Greening begins in late April, the peak of green is mid-May, and browning is well advanced by the end of August (Fig 5.2). Phenology may be controlled by soil temperature, soil water, or daylength. Greening before April is likely restricted by spring temperature (soil rises above 10C in April) rather than soil water (since all water potentials are always greater than -0.5 Mpa, Fig 5.2). Browning is likely limited by water exhaustion (since water potentials drop all summer, Fig 5.2) rather than temperature, which doesn't fall until browning is well underway. However, because some green is retained well into autumn, its final loss may be induced by cold temperatures (Fig 5.2). Daylength influences, rarely considered, may be important (Larcher 1995).

Soil temperature and soil water might be changed by type conversion, if for example, one vegetation type shades the ground surface or captures more drifting snow. We evaluate differences in three ways. 1) Summary of temperature/water data across months suggests that soils (15cm) under mixed grass prairie are warmer and drier than those under snowberry (Tables 5.3 & 5.4). While soil water early in the season may not differ between brome and snowberry, soil temperatures seem to be warmer than those under snowberry (Tables 5.3 & 5.4). 2) Graphs of the data (Fig 5.1) show that temperature differences begin to appear in late May and are distinct by late June. Soil water potentials are distinct by late June. Native vegetation is distinctly dryer in July and August (Tables 5.3 & 5.4). 3) Regression models predicting soil water from season (day), vegetation type, and years since last burned show significant effects of vegetation on temperature ($p=0.004$) and water ($p=0.039$) as previously stated.

Table 5.3. Vegetation and soil characteristics of native, snowberry, and brome stands.

Soil Water ²				Soil Temperature ³		
Types ¹	NAT	SNO	BROME	NAT	SNO	BROME
April	-0.01	-0.00	-0.00	6.7	4.7	4.9
May	-0.00	-0.01	-0.01	11.4	9.9	10.6
June	-0.67	-0.03	-0.39	14.1	12.7	12.8
July	-3.46	-2.37	-2.85	17.9	16.0	17.4
Aug	-3.57	-2.22	-1.85	16.9	15.9	16.6

1. Types are defined as one of five vegetation types(NAT= native grass sites on slopes sites between the bottoms and ridgetops, sno=snowberry clones, & brome=smooth brome clones.
2. Soil water is measured at a depth of 15 cm in megapascals.
3. Soil temperature is measured at 15 cm in degrees Celcius.

Table 5.4. Regressions of soil temperature and water at mid slope versus day, day*day, and time since burn comparing all three types of vegetation.

Soil Water (mgpascals)			Soil temperature(C)	
	Coefficient	P(2 Tail)	Coefficient	P(2 Tail)
CONSTANT	6.46197	P<0.001	-43.92925	P=0.001
DAY ¹	-0.0544	P<0.001	0.61777	P=0.001
TYPE ²	-1.0169	P=0.039	-0.39390	P=0.004
DAY2 ³	-----	-----	-0.00153	P=0.001
YRS ⁴	0.02516	P<0.001	-0.02351	P=0.001
DAY*TYPE ⁵	0.00679	P=0.006	-----	-----
Adj. R ² : 0.40005			Adj.R ² :0.68516	

1. Day of season measured in Julian Day.
2. Type is the type of vegetation (eg native, snowberry clones, or brome clones)
3. Square of Julian day created by multiplying day times day.
4. Yrs is the number of years since the site was last burned
5. Day*Type is an interaction term created by multiplying Day*Type of vegetation.

Table 5.5. Soil properties of mid slope Lostwood soils by vegetation type.

	Native	Snowberry	Brome	P level ¹
Texture				
% clay	17 $\pm$ 1.8A	15 $\pm$ 1.8A	14 $\pm$ 1.8A	P=0.254, F=1.43,30df
% sand	48 $\pm$ 4A	52 $\pm$ 4A	51 $\pm$ 4A	P=0.620, F=1.33,30df
EC	417 $\pm$ 6.8A	360 $\pm$ 6.8A	476 $\pm$ 6.8B	P=0.054, F=3.31,23df
PH	6.8 $\pm$ 0.1A	6.5 $\pm$ 0.1A	6.8 $\pm$ 0.1A	P=0.255, F=1.45, 23df
Carbon(%)	4.6 $\pm$ 0.4A	5.6 $\pm$ 0.4A	4.7 $\pm$ 0.4A	P=0.094, F=2.61,24df
Nitrogen(%)	0.419 $\pm$ 0.02A	0.478 $\pm$ 0.02A	0.424 $\pm$ 0.02A	P=0.131, F=2.21,24df
C/N ratio	11.7 $\pm$ 0.1B	11.7 $\pm$ 0.1B	11.2 $\pm$ 0.1A	P=0.024, F=4.37,24df

1. P level is the probability that there is a difference between vegetation types (native, snowberry, or brome). Values followed by different letters are significantly different at the p=0.05 probability level.

Table 5.6. Chemical properties of end of season standing crop at mid slopes on Lostwood NWR

	Native	Snowberry	Brome	P level ¹
Carbon	45.4 $\pm$ 0.3A	48.0 $\pm$ 0.3B	44.6 $\pm$ 0.3A	P=0.0001, F=50.56,21df
Nitrogen	1.30 $\pm$ 0.16B	1.24 $\pm$ 0.16B	1.01 $\pm$ 0.16A	P=0.029, F=6.71,21df
C/N	30.63 $\pm$ 3.69A	39.25 $\pm$ 3.69A	50.34 $\pm$ 3.69B	p=0.004, F=7.18,21df

1. Means followed by different letters are significantly different at p= 0.05 level.

One expects temperature and moisture influences to increase with time-since-fire because shading (heat reduction) and water capture (snow) effects should increase with increasing vegetation bulk. The regression models (Table 5.4) shows such changes ($p=0.001$) for both temperature and water. Because glacial-till soils of our mixed grass environment were mixed in transport, we expect them to have been identical initially. The near identity of sand, silt, and clay contents (Table 5.5) supports this hypothesis.

Because soils of our three vegetation types have been occupied by different vegetation their chemistries may have been modified by the plants (Jenny 1980). 1) Two changes might be attributed to leaching associated with the snow capture of taller plants. Electrical conductivity (salinity) decreases from Brome to mixed grass and snowberry (Table 5.5), as if salts have been leached out. PH is slightly lower under Snowberry than the mixed grass or Brome stands; however, this difference was not significant (Table 5.5, $P=0.255$). Generally, nitrogen and carbon were similar among all types. Soils under Brome were significantly lower in their C/N ratios ($P=0.024$).

Discussion

When a vigorous clonal species invades a grassland diversity falls sharply. Richness in mixed grass prairie may be 50 to 84 species (Weaver & Bruner 1954; Coupland 1950; Knight 1994) while we found 27 species on our North Dakota stands (Table 5.1). Richness in our brome and snowberry stands was 21 and 18 species (Table 5.1). Consequences of reduced richness include reduction in the variety of products and phenologic compression. Reduced variety of leaf, flower, and seed production could impact invertebrates, small mammals, and birds requiring or avoiding particular species. Replacement of many species with one species is likely to shorten the season by eliminating early and/or late species. Any animal not able to move to different vegetation (ie. possibly invertebrates to cattle) could be faced with seasons of feast or famine.

While we have not measured differences in community structure they obviously exist. 1) Shrubs provide a raised canopy not seen in mixed grass or brome. This provides raised perches for small birds (tops), cover for small mammals and birds (understory), and cover for larger animals (eg. deer). 2) Brome is more laterally homogeneous than mixed grass and, while taller, it provide poorer visual cover for small mammals and birds. 3) When clones, especially snowberry, occupy a small fraction of the landscape

(perhaps 10%) they add structural diversity likely beneficial to mobile animals from birds and small mammals to deer. If the clones spread to occupy a large percentage of the landscape, however, they reduce diversity, in part due to their own homogeneity.

Forage production increases from mixed grass and snowberry to brome. Forage quality differs little between mixed grass and brome since 'hay' is the product and protein contents are similar (Table 5.6). While their protein contents are similar, snowberry forage includes small twigs and tougher leaves more favorable to deer than cattle and small mammals. The raised canopy of snowberry is also less accessible to some grazers (eg. rabbits). We hypothesize that flower, fruit and seed production are higher in mixed grass than in brome and snowberry—because the clonal species probably allocate a much larger fraction of their photosynthate to rhizomes than mixed grasses do.

Phenology involves coordination of plant growth pulses with season (time and environmental condition). 1) Greening and browning of the three communities are parallel (Fig. 5.2) and are well adapted to growing conditions or by daylength. 2) Because of reduced diversity of clonal vegetation, we hypothesize a shortened flowering period. As a result, generalist pollinators in areas dominated by snowberry must experience spring/fall seasons of famine and feast during snowberry bloom (mid-May to mid-August, Pelton 1953). Replacement of diverse mixed grass vegetation with a single wind pollinated (Smooth Brome) must have a still greater impact. 3) Diversity of flowering time is associated with diversity of fruiting time. Animals dependent on ongoing seed production (as opposed to storage) may be threatened by compression of seed production season (with or without any change in total annual fruit yield).

Micro/meso environments are modified by invading vegetation. 1) The temperature decline under snowberry (Fig. 5.2) parallels the well known declines in temperature between canopy top and understory of forest stands (Fitzjarrald & Moore 1995). We attribute the greater supply of soil water under brome and snowberry to capture of snow. Such capture has been observed in other shrublands (Branson et al. 1981). This capture may rise as shrubs grow larger (long after fire) and decline as clone dominance increases from say 10 to 80% as grassy areas shrink and shrubby deposit areas grow. 3) When small water capturing patches exist for long periods soil quality may be modified. Ongoing leaching may change soil quality. We saw reduction of conductivity under snowberry and brome (Table 5.5), as if salts were leached by captured

water and/or capillary rise decreased with reduced surface temperature (reduced surface evaporation).

Accumulation of carbonates could account for our failure to see the drop in pH we expected to accompany the leaching induced drop in conductivity (West 2000).

Our comparison of these systems has assumed that differences are induced by vegetation rather than environment. Selection of paired stands insures comparable macro-environment. Choice of plot-groups with the same aspect and altitude (isoline) in each block insures similar microenvironment. Location of sites on slopes in a rolling moraine landscape insures that the soils were well drained (sandy, Table 5.5) and well above the water table. The uniformity of texture of texture across vegetation (Table 5.5) substantiates the hypothesized of soils mixed in transit across the Canadian prairies.

Conclusion

The three general vegetation types we studied (native, brome, and snowberry) grew in similar soils that had minor differences in physical characteristics that may be caused by the invading plant rather than as a pre-existing geological characteristic of the soil (Nikiforoff 1938; Koelling & Kucera 1965; Risser & Parton 1982; Buyanovsky et al 1987; Groffman et al 1993). All three occupied soils with similar moisture early in the summer. Later in the growing season native stands became dryer than the other two vegetation types. Smooth Brome is a cool season grass which came from areas with similar climates to the northern Great Plains and seems to be very well adapted to this region (Dayton 1948; Stubbendieck et al.1992). Moisture and competition from established plants may limit brome and snowberry invasion from bottoms and hilltops (Bonser,& Reader 1995; Burke & Grime 1996; Foster 1999, 2000). Smooth Brome may be sensitive to early spring burning which could make spring burning a useful tool to limit its increase in the landscape (Collins 1987; Hobbs & Huenneke 1992). Snowberry will likely increase until it is removed or reduced by fire or chemical removal or limited by its water requirements (Pelton 1958; Collins & Gibson 1990; Collins & Wallace 1990). Periodic prairie fires (natural or prescribed) may be the only inexpensive way to reduce both species to retain the diversity of mixed-grass prairie on Lostwood National Wildlife Refuge.

We concentrated our study upon grassland types. Our shrub standing crop estimates gave us only estimates of leaf and new twig production. This under-estimates total standing crop because stem diameter increase is not included in the standing crop. Future study should include stem biomass in the standing crop estimates.

We limited our type conversion studies to snowberry and brome. Kentucky Bluegrass is another exotic plant that is increasing in our prairies. Future studies of type conversion on mixed grass prairie types to other vegetation need to include this plant.

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CHAPTER 6

EFFECT OF FIRE AND VEGETATION TYPE ON
INVADABILITY IN NORTHERN PRAIRIES-- A PHYTOMETER ESTIMATE.

Introduction

Landscapes usually contain a diversity of communities, presumably with different susceptibilities to weed invasion. Causes for differences in susceptibility might be five, or more: 1) Rich segments of a resource gradient can be more (Hobbs & Huenneke 1992; Burke and Grime 1996; Maron & Connors 1996; White et al 1997) or less (Foster 2000; Brown et al 1998) invadable than poorer segments, likely depending on the productivity of the invader relative to members of the community invaded. 2) Structurally different communities (eg different crops, Weaver & Dale 1974; Bazzaz 1991; Tilman 1997) occupying a single physical environment may have different invaders. 3) Invasion resistance seems to be proportional to diversity of species or functional groups, that is the fraction of the niche space filled (Tilman 1997; Naeem et al 2000; Symstad 2000; Dukes 2001). 4) While plowing usually favors invasion, the effect of less drastic disturbance varies with the species involved. Soil disturbance usually favors invasion (Hobbs & Mooney 1991; Hobbs & Huenneke 1992; Burke & Grime 1996; Zink et al 1998). Grazing may favor invasion (Hobbs & Huenneke 1992), disfavor it (Hobbs & Huenneke 1992) or leave it unaffected (Brown & Archer 1999; Brown et al 1998; Sheley et al 1997) and cessation of grazing may favor invasion (Morris et al 1992; Costello & Lunt 2000). Invasion may be stimulated (Hobbs & Huenneke 1992) or inhibited (Hobbs & Huenneke 1992; Smith & Knapp 2001; Morgan & Lunt 1999) by fire and stimulated by its cessation (Costello & Lunt 2000). 5) Whatever a unit's susceptibility, realization of potential invadability is proportional to dispersal of propagules to the unit (Morgan 1998; Tyser & Worley 1992; Tilman 1997; Smith & Knapp 2001).

Diverse communities of the northern pothole prairie (the Missouri Coteau) are closely juxtaposed - thus facilitating comparison (eg. of invadabilities) of widespread vegetation types which differ in resource availability, vegetation structure, and disturbance. In this landscape, a topo-gradient runs from relatively moist bottoms (tallgrass prairie) through mixed grass prairie to dry upland (shortgrass) sites (Weaver &

Fitzpatrick 1934; Weaver 1968 ; Bragg & Steuter 1996; Simms & Risser 2000). In the midslope mixed grass prairie environment one finds grassland invaded by clones of exotic grass (*Bromus inermis*, *Poa pratensis*), native shrubs (*Symphoricarpos occidentalis*), and native trees (*Populus tremuloides*). At Lostwood National Wildlife Refuge prescribed burning has provided examples of each type in recently burned (1-2 years) through long unburned (> 50 fire free years) condition.

One might compare the invadability of communities occupying different segments of the northern plains landscape by comparing the invasion which has occurred on them. Study of 'natural' invasion is suboptimal, however, because seeds are rare and unevenly dispersed in our relatively weed free landscape. Therefore, we seek to compare the relative invadabilities of our communities with phyto-meters (Weaver & Clements 1938; Payson 1996), weeds introduced to compare the degree to which different communities exclude them competitively. We tested a proxy grass and a proxy forb as indicators (meters) of invadability, instead of noxious weeds, both because the proxies should react in similar ways to competition from the invaded community and because managers of the grassland would not allow introduction of noxious weed 'phytometers'.

Methods

Study Sites.

The study was conducted on the Lostwood National Wildlife Refuge (NWR), near Stanley North Dakota. While the refuge enjoys a single mixed grass prairie climate (Weaver 1980; Kruse & Bowen 1996; Coupland 1950, 1961; Bragg & Steuter 1996; Simms & Risser 2000), its rolling topography creates diverse microclimates and diverse vegetation (U.S. Fish & Wildlife Service 1998). That topography results from Lostwood's location on the terminal moraine of the continental glacier, the 'Missouri Coteau', and includes alternating dry hilltops and pothole bottoms which often contain ponds or wetlands (Pielou 1991, 1998). Microclimates resulting from the rolling topography support juxtaposed tallgrass (bottoms), mixed grass (slopes) and shortgrass (hilltops) vegetation. Besides mixed grass prairie, midslope sites support invading clones of exotic grasses (*Bromus inermis* and *Poa pratensis*) and native shrubs (*Symphoricarpos occidentalis*).

Gradients Studied.

Invadability was compared among stable communities distributed on three gradients. 1) To examine invadability on a resource richness gradient we compared sites on adjacent bottoms (tallgrass), slopes (mixed grass) and uplands (short grass). 2) To examine invadability of structurally diverse vegetation occupying sites with comparable resource richness, we compared invadability of sites in a mixed grass (slope) environment occupied by native grass, taller denser brome (*Bromus inermis*), and shrubby snowberry (*Symphoricarpos occidentalis*). 3) One also asks whether recently disturbed (unhealed) communities are especially susceptible to invasion. As one example, we compared the invadability of sites with recently burned versus long unburned stands of fire-adapted native grass.

Fire treatments were available at Lostwood, because fire and grazing were eliminated on the refuge from 1930-1972 and were gradually reintroduced by the manager (Karen Smith) with careful record keeping. Karen helped us locate eleven slopes burned (2, 3, 4, 6, 11, to more than fifty years ago) or 'experimental comparison' of the invadability of recently burned and long unburned sites.

On each of the eight slopes, three topographically distinct sites were selected to compare invadability of communities occupying a richness ('water') gradient paralleling that of the northern plains. A low site lay in tall grass prairie (*Andropogon gerardii*), a mid-slope site lay in mixed grass (*Schizachyrium scoparium*) and an upland site lay in shortgrass prairie (*Bouteloua gracilis*/ *Stipa comata*). The sites lay within 50m of one-another. Table 6.1 summarizes environmental changes on this gradient.

In the mid-slope (mixed grass) segment of the topographic gradient examples of three community types were selected for comparing invadability of distinct vegetation types occupying a single environment. The first was the 'natural' mixed grass prairie, the second lay in an invader clone of brome (*Bromus inermis*), and the third lay in an invader clone of snowberry (*Symphoricarpos occidentalis*). Brome is an exotic (Russian) pasture grass so well adapted to the mixed grass climate that it escapes from cultivation (Dayton 1948; Stubbendick et al 1997). Snowberry is a native shrub which tends to invade and dominate mixed grass prairie native grass when fire is excluded (Coupland 1950; Pelton 1958; Collins & Gibson 1990; Collins & Wallace 1990).

Environments

Environmental changes on the topographic and vegetational gradients suspected from vegetational differences were verified with field sampling. 1) Soil water was measured periodically over three years using plaster blocks buried at 15cm (6 inches). The conductivity of the blocks was measured with an ohm-meter calibrated against blocks in soils with known water contents (Campbell & Gee 1986). 2) Soil temperature was measured simultaneously with thermocouples buried at 15 cm and a micro-voltmeter (Taylor & Jackson 1986). 3) Carbon, nitrogen, pH, and conductivity (salinity) of soil samples from each site were measured in the MSU soil testing lab as indicators of soil nutrients/toxicity. Carbon and nitrogen were measured with the LECO 2000 CNS (Nelson & Sommers 1996, Bremner 1996). Conductivity and pH were measured on 1:1 soil water slurries with appropriate meters (Thomas 1996 & Rhoades 1996). Soil texture was measured with the Boyoucos hydrometer method (Gee & Bauder 1986). 4) Photosynthetic standing crop was used as an index of vegetation competitiveness. All standing crop in two 30x60 cm quadrats was harvested, partitioned (grass, forb, and current shrub growth), dried, weighted, and expressed on a g/m² basis.

Phytometers

We used one grass (barley, *Hordeum vulgare*, var Stark.) and one forb (sunflower, *Helianthus annuus*) as phytometers, because they model herbaceous invaders. As non-invasive plants, both plants were acceptable to managers of native grasslands. That the phytometers are adapted to the physical environment of the region was shown by the fact that both are cultivated in un-irrigated fields of the region. Thus, by introducing them into various communities, we intended to test the capacity of plants in the grass and forb guilds to competitively establish in representative segments of the three gradients described below. We hoped that, with its diffuse root system and basal leaves, barley would represent the competitive strategy of invading grasses generally. Similarly, with its taproot system and apical leaves, sunflower was intended to represent the competitive strategy of invading forbs generally. We expect this representation to apply well in early summer, when water is relatively abundant (Table 6.1) and all plants vie for access to light and soil resources. The model may deteriorate as the season progresses and plants of different guilds increasingly allocate photosynthates differently to seed (annuals), root reserves (perennials), or stems (fire intolerant

over-arching shrubs and trees). Thus, while our annual phytometers may indicate the capacity of invaders to establish in vegetation of different types, other tests must determine the long term success of perennials. Perennial invaders, the primary pests of the northern mixed grass prairie, include grasses (*Poa pratensis* and *Bromus inermis*), forbs (*Euphorbia escula* and *Melilotus officinale*) and woody plants (*Symphoricarpos occidentalis* and *Populus tremuloides*).

Plants used as phytometers have been introduced as seeds [to compare resistance of various vegetation types to plants in early stages of growth (Weaver & Clements 1938; Payson 1996; Burke & Grime 1996; Tilman 1997; Brown et al 1998; Brown & Archer 1999; Foster 2000; Naeem 2000)] or as older plants [to by-pass the establishment stage and compare resistance of the vegetation types to persistence of more established plants (Weaver & Clements 1938; White et al 1997; Foster 1999)]. We planted seeds. At each site ten holes evenly spaced on a 2 meter line were prepared for planting. Each hole was cored with a tulip planter (6.3 cm diameter x 10 cm deep), soils were crumpled, and major plant parts (large roots, rhizomes, and root crowns) were removed. In mid-May five holes were planted to barley and five to sunflower. Approximately five seeds were planted at two cm in each hole and the soil was packed. After germination, the population in each hole was thinned to the strongest three seedlings. In August all plants were measured, harvested, dried, and weighed individually. Measures were height, diameter, and weight.

Statistics

Systat (SPSS, Inc 2000) was used to make our statistical analysis which included multiple regressions and ANOVA in our analysis.

Results and Discussion

Invadability of Vegetation, General

The invadability of vegetation on topographic, standing crop, and community vigor gradients was compared by seeding a forb (sunflower) and a grass (barley) into micro-disturbances in diverse communities at (8 sites). Seedling survival was generally poor (22-43%, Table 6.2). Growth was poor, with plant heights rarely reaching 20 cm (Table 6.2). We conclude that invasion of (establishment in) closed communities is difficult regardless of resource availability on site, vegetation occupying the site, or time-since-fire. In our experience, the competition which limits invasion is significantly reduced only when established vegetation is removed (disturbed) in areas large enough to prevent its continued dominance through lateral root growth ($> 1000 \text{ cm}^2$; Peyson 1996).

Invadability on Environmental Gradients

Trends in plant performance on the three gradients studied (Tables 6. 2 and 6.3) were weak (statistically insignificant). Never-the-less, the following paragraphs examine these trends as hypothesis generating material .

On the topographic gradient, vegetation grades from tall grass through mixed grass to shortgrass, with a corresponding decline in productivity. We attribute the declining productivity/standing crop to declining water availability (progressive drying and warming, Table 6.1), rather than the secondary decline in nutrient availability (nitrogen, Table 6.1). 1) Survivorship is erratic for sunflower and tends to rise upslope for barley. 2) Weights attained by survivors are highest at midslope for both sunflower and barley, as if both species compete poorly with tall grass vegetation and grow poorly with the limited resources of the shortgrass environment.

Table 6.1. Environment of three topographic gradients and two additional vegetational types.

TYPES ¹	BOT	MID	TOP	PROB	MID	BRM	SNO	PROB
<i>Competition</i>								
SC ³ , gm/m ²	268C	207B	141A	0.001,82,254df	207A	259B	204A	0.02,3.95,108df
<i>Soil water potential (megaPascals)</i>								
April	0	-0.01	-0.02		-0.01	0.00	0.00	
May	0	0	-0.28		0.00	-0.01	-0.01	
June	-0.29	-0.67	-1.14		-0.67	-0.39	-0.03	
July	-1.2	-3.46	-3.08		-3.46	-2.85	-2.37	
Aug	-1.91	-3.57	-4.39		-3.57	-1.85	-2.22	
<i>Soil temperature(C)</i>								
April	5.7	6.7	7		6.7	4.9	4.7	
May	10.7	11.4	12.1		11.4	10.6	9.9	
June	13.6	14.1	14.9		14.1	12.8	12.7	
July	17	17.9	18.9		17.9	17.4	16.0	
Aug	16.6	16.9	17.9		16.9	16.6	15.9	
<i>Soil texture and chemistry</i>								
% clay ³	16A	17A	19A	0.61,0.72,30df	17A	14A	15A	0.25,1.43,30df
% sand	53A	48A	46A	0.83,0.18,30df	48A	51A	52A	0.72,0.33,30df
EC	468A	417A	508A	0.23,1.53,30df	417A	476B	360A	0.05,3.31,23df
pH	6.7A	6.8A	7.0A	0.55,0.54,30df	6.8A	6.8A	6.5A	0.25,1.45,23df
carbon(%)	6.3A	4.6A	3.8A	0.001,8.34,30df	4.6A	4.7A	5.6A	0.09,2.61,24df
nitrogen(%)	0.54A	0.42A	0.36B	0.01,3.02,30df	0.42A	0.42A	0.48A	0.13,2.21,24df
C/N ratio	12.8A	11.7A	11.6A	0.06,3.02,30df	11.7A	11.2B	11.7A	0.02,4.37,24df

1. Types are defined as one of five vegetation types(bottom=hill base, mid= on slopes, top=ridgetops, Sno=*Symphoricarpos occidentalis* (snowberry), and Brm= *Bromus inermis* (smooth brome)

1. Soil water(mgpascals) and temperature(°C) were measured at 15cm soil depth.
2. Means with different letters following are different at p=0.05 level. Probability order is p value, F statistic, and degrees of freedom.

Table 6.2. Performance of invading phytometers (sunflower and barley) on the resource (topographic) gradient.

Topo-position	BOT	MID	TOP	PROB	BOT	MID	TOP	PROB
<i>Sunflower performance</i>					<i>Barley performance</i>			
Measures of success								
% survival ¹	37A	26A	38A	0.17, 1.87,37df	27A	31A	43A	0.20,1.68,60df
Wt/plot (gm) ²	5.6A	4.3A	2.9A	0.29, 0.45,37df	1.3A	1.5A	1.1A	0.78,0.25,34df
Wt/plant (gm) ³	0.65A	1.10A	0.49A	0.49, 0.72,36df	0.26A	0.29A	0.21A	0.78,0.25,34df
Adaptation via allocation.								
Ht ⁴ (cm)	22.2A	19.9A	16.9A	0.23,1.49,37df	15.5B	11.1A	9.5A	0.04,3.37,60df
Dia ⁵ (cm)	0.09A	0.10A	0.10A	0.76,0.31,31df	0.03A	0.03A	0.04B	0.03,4.02,34df
Gm/cm	0.03A	0.04A	0.03A	0.76,0.39,24df	0.01A	0.02A	0.02A	0.59,0.54,34df

1. % survival is the total number of survivors/15 seeds planted.
2. Wt/plot is the total weight of all surviving plants of 15 planted.
3. Wt/plant is the total weight divided by number of survivors.
4. Ht=average height of survivors of 15 planted.
5. Dia=average diameter of survivors.

Table 6.3. Regression analysis of the effect of time of season, topographic level, time since burned, and the type of plant on temperature and soil water.

Soil Temperature			Water	
	Coefficient	Probability	Coefficient	Probability
CONSTANT	-46.30095	0.00001	4.63640	0.00001
Julian Day	0.64457	0.00001	-0.04229	0.00001
Julian Day Squared	-0.00160	0.00001	-----	-----
Topo level ¹	0.79513	0.00001	-0.74961	0.00001
Times since burned	-0.01494	0.00001	0.01125	0.00004
Species ²	-0.45739	0.00027	0.20519	0.05702
Adj. R ² : 0.699 Standard error : 2.43			Adj. R ² : 0.365 Standard error: 2.09	

1. Topo levels are bottom of the hill, mid slope, and top of the hill. These are coded -1, 0, 1.
2. Species are native, *Symphoricarpos occidentalis*, and *Bromus inermis*. They were coded 1, 2, and 3.

Human influence has converted much of the mixed grass prairie to either exotic plants such as *Bromus inermis* (via exotic introduction, Coupland 1961; Wilson & Belcher 1989; U.S. Fish & Wildlife Service 1998) or *Symphoricarpos occidentalis* (via fire protection, Pelton 1958; U.S. Fish & Wildlife Service 1998). Vegetation differences appearing in the once uniformly vegetated mixed grass environment might generate environmental differences influencing invadability. Affective changes may include reduced ground level sunlight (O'Conner 1995), reduced soil temperature (Table 6.1), increased soil water (Table 6.1), or biological characteristics (eg allelopathy) of the communities. 1) On the gradient from low to high standing crop survivorship declined for the forb (sunflower) and increased for the grass (barley). 2) Among the three vegetation types, the site best for sunflower growth (snowberry) was worst for barley. And the site worst for sunflower (brome) was best for barley. This suggests a basic difference between our forb and grass invaders, see below. Specifically, on our sites the gradient in standing crop from low (mixed grass) through brome, to high (snowberry) associates more with reduced evaporation (reduced insolation and wind flow) than with increased transpiration. This makes soils under the invading vegetation slightly cooler and moister than under mixed grass (Table 5.1).

It is speculated (Collins 1987; Bragg 1995) that fire weakens established plants and eases the entry of colonizers into grasslands (of grazing effect, Mueggler 1977). 1) Survivorship of our forb (sunflower) was unaffected by time-since-fire (Table 6.3), while survivorship of our grass (barley) tended to rise with time-since-fire (Table 6.3). 2) Growth of our forb was erratic on the time-since-fire gradient (was highest on recent and old burns), while growth of our grass (barley) tended to increase with time-since-fire (Table 6.3). 3). Neither (insignificant) trend supports our hypothesis.

Intrusiveness of Guilds

Comparison of sunflower (forb) and barley (grass) responses on the three gradients demonstrates differences between the species. Parallel experiments could determine whether they extend to the forb and grass 'guilds'. 1) Sunflower survivorship varied little on any gradient. While barley survivorship increased with increasing stress on all gradients. Are grass seedlings generally more tolerant of stress than forb seedlings? 2) On the resource gradient surviving sunflower and barley seedlings produced similarly, with worst performance at hilltop and best on the slope. Do forbs and grasses generally show similar responses

to resource availability? 3) Among vegetation types sunflower and barley produced differently. Sunflower was better adapted to growth with snowberry than barley was, likely because leaves produced at the sunflower apex are higher in the canopy and absorb more light than do barley leaves growing from basal meristems (Grime 1979). Sunflower was less adapted to growth with brome than barley was. This is contrary to our expectation that the forb (sunflower) would establish better in grassy vegetation (brome) than the grass (barley), because apical growth would expose the forb's leaves higher in the canopy and its roots deeper in the soil than the grass's (Grime 1979; Walter 1984). Perhaps sunflower is less tolerant of brome allelotoxins than barley is. 4) On the community condition (vigor) gradient, barley growth was worst on recently burned vegetation, as if its seedlings didn't tolerate drying sun and wind. Sunflower grew well (1-2 yrs) or poorly (3-5 yrs) on recent burns. Both invaders grew best in long unburned vegetation (11-50 yrs). If growth becomes easier as time since burn increases, the value of shelter (from sun, wind, and drought?) may exceed the cost of competition with unburned plants. An alternative interpretation is that competition is most vigorous in just burned stands (barley) or recently burned stands (sunflower) stands and least in long unburned stands (Morgan & Lunt 1999).

Conclusions

1) Our plants are intended to model invasion of forb and grass invaders. Sunflower and barley establishment should be equal to or stronger than average invaders in the moist soil season (May-July), because large seeds provide for strong initial growth (Burke and Grime 1996). In the post-establishment period (August-September) behaviour of our annuals will deviate from perennial invaders; they allocate photosynthates to seeds rather than perennating organs (roots and shoots). 2) Despite indications that empty niches exist in undisturbed grassland (Tilman 1997), the species we introduced showed low survivorship and poor growth. 3) Survivorship of sunflower varied little on stress gradients, while survivorship of barley seemed to increase with stress. 4) Growth of sunflower and barley varied on all three gradients. Both plants grew best at the center of the resource gradient. Sunflower grew worst with grass(brome) and best with a shrub (snowberry), while barley responses were opposite. While plant establishment may be hard (barley) or easy (sunflower) on recently burned sites, it is uniformly easy in old

grasslands. 5) Smaller seeded plants might have shown larger differences in survivorship and growth on our gradients (Burke and Grime 1996). 6) Performance of other forb and grass species should be measured to determine whether differences between sunflower and barley can be generalized to forb and grass 'guilds'.

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CHAPTER 7

ESTIMATING COMPONENTS OF END-OF-SEASON BIOMASS WITH
REFLECTANCE IN MULTISPECTRAL WAVEBANDS, NORTHERN GRASSLANDSIntroduction

Managers need estimates of end-of-season standing crop to estimate winter forage availability, summer-fall fire conditions, and fall-winter cover for wildlife. Estimates made from pre-season rainfall predict end-of-season standing crops remarkably well (Smoliak 1956) -- presumably because pre-season conditions determine/forecast vegetation performance in the early/mid seasons which determine/forecast end of season standing crop, in turn. Local areas within the same precipitation zone limit pre-season rainfall use. However, because the measurement of soil water is intensive/expensive, in an extensive or diverse landscape we seek an analogous predictor which is less expensively measured over broad areas. Satellite imagery provides a likely tool (hypothesis 1), because reflectance indicates the condition of early season vegetation (Aase et al 1987; Paruelo & Laurenroth 1995; Tiesen et al 1997; Wessman et al. 1997; Bork et al. 1999)-- thereby incorporating more factors (water and others) and measuring their integrated effect more directly. Such reflectance data may be usefully supplemented with other geographic data (eg, topography, burn history, and grazing history, hypothesis 2) or spectral data from other seasons (hypothesis 3).

To test the first hypothesis we tested reflectance as an indicator of end-of-season standing crop. Landsat wavebands were examined because, while they contain less information than hyper-spectral images, they are inexpensive and are potentially available for any time period from various radiometers—Landsat, Ikonos, or hand-held radiometers (van Leeuwen & Huete 1997; Goodin & Henebry 1997; Davidson & Csillag 2001). Single bands provide some information about chlorophyll reflectance (green), chlorophyll reflectance (red), and cell wall absorbance (Nir), and thus for biomass. These correlations form the basis for prediction of total biomass from reflected light (Paruelo & Laurenroth 1995; Wessman et al. 1997; Bork et al. 1999) and may be useful for prediction of other components of biomass as well (Wessman et al. 1997; Bork et al. 1999). Information gained can sometimes be increased by combining these data in

multiple regressions, ratios, or combinations of these. Of the several ratios tried (DVI, RVI, NDVI, SAVI), (Aase et al. 1987; Bork et al. 1997; Davidson & Csillag 2001) the most useful has been NDVI (Paruelo & Laurenroth 1995; van Leeuwen & Huete 1997; Goodin & Henebry 1997; Davidson & Csillag 2001).

We tested two extensions of these conventional methods. First, we tested the hypothesis (#2) that inclusion of indices of topography, fire history, and grazing history will likely improve prediction of end-of-season standing crop. For example, pasture records of recent burning or grazing should predict lowered standing dead and litter. Topographic records available from digital elevation models, if available, should contrast the richer (low sites with more rainfall run-in and less wind/ evaporation) and poorer (hilltop) microenvironments. Second, we tested the possibility (hypothesis 3) that combination of spectral data from several dates would predict end-of- season biomasses better than data from a single date.

Thus our objectives were to test several spatially extensive predictors of end-of-season standing crop--specifically to evaluate remote sensing made at different seasons and to determine whether supplemental data (indices of fire/grazing history and topography) improve predictions of any of these regressions, and to measure improvement in estimates when images from several seasons are used simultaneously.

Methods

We tested our capacity to predict standing crop and standing crop components from measures of reflectance in Landsat wavebands under three conditions. First, we examined reflectance in three vegetation types (short, mixed, and tall grass vegetation). Second, since the manager might use images from different seasons or from several seasons, we compare the usefulness of data gathered in six different periods (fortnights)-- and data combined across those six periods, as a maximum conceivable image set. Third, since a manager might have supplemental data (eg topography, grazing history, and fire history), we examined the value of including such data in estimating standing crop.

To test the usefulness of reflectance measures of biomass in different vegetation types, we chose a landscape with a large natural diversity. Our studies were conducted on the Lostwood National Wildlife Refuge, Kenmare, North Dakota. The refuge lies on the Missouri Coteau, the terminal moraine of the continental glacier (Coupland 1950; Pielou 1991). Its rolling topography presents potholes and lakes, low

(tall-grass), slope (mixed grass often with inclusions of aspen or shrubs), and hilltop (short grass) grasslands. We compared reflectance of grasslands occupying low, mid-slope, and high segments) of eleven representative transects, that is, a total of thirty-three sites. Our sites received zero to light grazing during the previous ten years (1989-1998) before our measurements and no grazing during the measurement period (1998-2000, Table 7.1).

To examine the effects of time since fire on biomass (mostly accumulation of litter) and reflectance, transects were chosen to represent a range of recently burned and long unburned sites (1 to over 50 years without a fire ,Table 7.1). Similar data are available to land managers who have recorded dates of the last several fires on a site.

To determine our capacity to measure grazing effects (mostly reduction of litter and standing crop) we added simulated grazing treatments at each of the thirty-three sites described above. At each site we staked three 3x4m plots side-by-side on the contour with a meter wide buffer between the plots. After staking, treatments 1-3 were randomly assigned to the plots. The first treatment was ungrazed (untreated). In the second plot, standing dead was removed in the spring by mowing to 3 cm with a 'weed whip' and raking it off without disturbing the litter. In the third plot standing dead was cut and both it and litter were vigorously raked out. These treatments approximate 'moderate grazing' which removes most standing crop and heavy grazing which removes both standing crop and litter (Aldous 1930; Penfound 1964; Sims and Singh 1978 ; Hulbert 1969, 1988; Heitschmidt et al 1989; Ralphs et al 1990; Biondini et al 1998).

Biomass was measured, by component, in eleven sites on three topographic positions as follows. 1) Current production in the ungrazed, moderately grazed, and heavily grazed plots at each of the thirty-three sites was sampled in all 3x4m plots with an August harvest (1998, 1999, and 2000); material in two 30 x 60 cm (1x2 foot) plots, forage clipped, dried, weighed, and data were scaled up to g/m^2 . 2) Spring standing dead was estimated in 2000 by cutting all forage in the moderately grazed plot to 3 cm with a weed whip, collecting it with a broom rake, weighing wet, and using the dry wt/wet weight of a 10% sample to adjust wet weight to dry weight. 3) Litter was estimated in spring 2000 by cutting and measuring standing crop (as above) then vigorously raking the 3x4m plot to collect all litter. Litter dry weight was estimated by weighing the litter wet, sampling (10%), and multiplying total weight by the dry weight/ wet weight ratio of

the sample to find the dry weight. Because vigorous raking also captured soil, the dry weight was further corrected by sub-sampling (33%), ashing, and multiplying estimated dry weight by (sample weight - ash weight)/ sample weight. 4) Fuel weight was estimated in two ways. A minimal estimate of fuel is litter plus current production (Table 7.1 , column 6). A maximal estimate, assuming that all spring standing dead from the previous year survives the summer, is litter plus standing dead plus current production (Table 7.1, column 7). The small amount of 'gray fiber' in the August clips indicates that the first estimate is most accurate.

Our predictor, reflectance, was measured periodically at each of the 99 sub-sites (11 units x 3 topographic positions x 3 grazing treatments) throughout the seasons of 1998, 1999, and 2000. 1) Eight, eight, and two dates were sampled respectively in 1998 (April 17-24, May 18-25, June 10-13, June 23-27, July 9-12, July 27-30, August 20-26, & September 12-15), 1999 (April 23-26, May 9-12, May 26-29, June 12-17, July 7-13, July 30-August 3, August 22-27, & Oct 30-Nov 3), and 2000 (May 3-7 & June 3-7). 2) Measurements were made with a 'Cropscan differential radiometer' which compares incoming radiation with reflected radiation in the blue (485 nm), green (560 nm), red (660 nm), near infrared (830 nm) and infrared (1650 nm) bands (Aase et al. 1987; Goodin & Henebry 1997). These wavebands are sufficiently similar to Landsat wavebands to allow extrapolation of our results to Landsat imagery. We also tested NDVI (normalized difference vegetation index, (NIR-Red)/(NIR + Red) (Wessman et al 1997; Davidson & Csillag 2001), since it is commonly a useful index of biomass present. 3) The usual precautions were taken to avoid biasing reflectance data. To minimize sun angle effects, measurements were made at mid-morning (9:00-11:00am) and mid-afternoon (1:30-5:00pm) only (Goodin & Henebry 1997). Measurements were not made on excessively cloudy days. Time of measurement was rotated among plots to remove variation associated with the time of measurement (day. reflectance variation.) We tested the effect of time of day on reflectance against time of day by a plot technique (Neter et al. 1990). We could not see an apparent time of day trend in the plots.

The power of reflectance to predict biomass was measured by regressing observed biomass against predictors ranging from five wavebands at each of six 'seasons', a combination of these wavebands across six seasons, and inclusion of supplemental data with single date images and multiple date images. In each case, we report the the best stepwise multiple regression.

Systat (SPSS,Inc 2000) was used to make these stepwise multiple regressions.

Results

Introduction

In this section we present models, with accuracy assessments (ie. adjusted R^2) for remotely predicting quantities of litter, current production, and total fuel. Subsections dealing with these components are all developed in three parallel stages. 1) Estimates made with reflected light alone are tested for each two-week segment of the summer. This analysis will suggest to a manager which season is most useful for a one-measure analysis and how much he can expect of it. 2) A manager might also ask whether supplemental data might improve predictions of standing crop. We evaluated the usefulness (R^2) of supplements including topography (available from a DEM), time since the site was last burned, and recent grazing history (both possibly available from management records). 3) With or without supplemental data (topography and fire/grazing history), one asks what additional information might be captured by combining data from images made at several times during the growing season. Thus, we evaluated (R^2) the use of six images (instead of one) both with and without supplemental data; the use of six images probably sets an upper limit for increasing resolution by integrating information across multiple images/ time periods.

Ground Litter

Stepwise regression of litter against the five reflectances (blue, green, red, near infrared, and infrared) and NDVI alone produced significant regressions, but with low predictive value (R^2 , Table 7.2). The highest R^2 s measured were in April, June, and autumn, not summer (0.16, Table 7.2). The most predictive wavelengths varied with season. Blue light was predictive from June 1 until July 20. Red and near infrared

wavelengths were predictive in early spring, June, July, and fall regression. NDVI was a significant factor in most useful regressions.

Adding topography, fire history, and grazing intensity improved the regressions to 0.40 - 0.46 (Table 7.2), ie by about 30%(40%-16%). The highest values appeared in late June and fall (August 10-November 1). Fire and grazing history improved the predictions in all time periods. The addition of topographic information improved predictions (R^2) both early (April to June 1) and late in the growing season.

Combined use of multiple (six) images obtained throughout the growing season might improve prediction of ground litter production still further. We tested this hypothesis by using all reflectance time periods as separate factors in a stepwise regression. 1) First, we tested the predictive capacity of the five wavebands alone integrated across six dates. The R^2 for the litter model was 0.40 (Table 7.3), an improvement of 24% (40%-16%) over the best single image estimate. In this model, the most useful wavelengths in the early season in this model were red, near infrared, and NDVI. After 1 July, blue, green, red, near infrared and NDVI were all significant factors in the best model. 2) Adding information on topography, fire history, and grazing level improved predictive capacity of the model still more. The adjusted R^2 rose to 0.605 (Table 7.3), an improvement of another 20% over multiple image predictions without fire history and grazing intensity in the model. In this model, fire history and grazing intensity were significant factors, but topographic position was not.

Current Years Production

End-of-season standing crop (production) was estimated first with data from one date only. When only the five spectral bands were used as predictors, adjusted r squared values ranged from 0.293 to 0.474 (Table 7.4). Predictions were best (R^2) in late June and fall. The blue wavelength was useful from April 25 until June 1. Red and near infrared wavelengths were useful in most periods. NDVI was useful during both spring and fall periods.

Table 7.1. Sample sites studied, their histories, vegetation types, topographic locations and biomass components.

Site	year last burned	std dead spr ¹ 2000	litter spr ² 2000	current prod ³ 98-'00	total fuel (L+C) ⁴	total fuel (L+C+SD) ⁵
<i>Top-Tall grass</i>						
Tower	1997	58	55	114	170	228
Iverson	1997	47	62	187	249	296
Aspen	1996	23	52	123	174	197
SC Core	1995	86	271	180	450	536
HQ-South	1995	128	178	140	318	446
NC Core	1995	39	51	136	187	226
Field 7	1994	35	138	104	242	277
T. Lake	1992	72	247	168	414	486
'87 Burn	1987	85	330	172	502	887
Wilderness	< 50	52	420	137	557	609
HQ-North	< 50	31	66	131	264	295
<i>Mid slope-mid grass</i>						
Tower	1997	75	63	220	283	358
Iverson	1997	113	668	190	857	970
Aspen	1996	105	71	218	289	394
SC Core	1995	105	131	139	270	375
HQ-South	1995	153	558	272	829	982
NC Core	1995	156	410	224	634	790
Field 7	1994	65	389	149	538	603
T. Lake	1992	98	207	221	427	705
'87 Burn	1987	97	247	142	390	487
Wilderness	< 50	22	326	214	539	561
HQ-North	< 50	153	598	198	796	949
<i>Bottom-tall grass</i>						
Tower	1997	235	183	320	333	568
Iverson	1997	35	3	181	184	219
Aspen	1996	114	166	217	383	497
SC Core	1995	38	120	219	338	376
HQ-South	1995	132	661	341	1002	1134
NC Core	1995	133	261	273	535	668
Field 7	1994	199	827	353	1181	1380
T. Lake	1992	75	142	234	376	451
'87 Burn	1987	89	290	316	606	695
Wilderness	< 50	121	679	311	991	1112
HQ-North	< 50	66	381	154	534	600

¹ Standing dead vegetation measured before the spring greenup.

² Biomass accumulated on the soil surface and measured before spring greenup.

³ Biomass produced plants during 1998, 1999, and 2000, harvested in August, and averaged.

⁴ Total fuel calculated by adding spring soil surface litter and current year's production.

⁵ Total fuel calculated by adding litter, spring standing dead and average production.

Supplementing spectral data with data on topography, burn history, and grazing generated R^2 of 0.34 to 0.51 (Table 7.4), an improvement of about 17% (51-34). The late June ($R^2=0.50$) and fall ($R^2=0.49$) periods continued to have the highest predictive power. However, while inclusion of site factors improved the predictions, we were still unable to predict over 50% of the variability of the end of season production.

Using six images well dispersed in the growing season improved predictions (adj R^2) approximately 15% (62-47). 1) Use of multiple acquisitions without supplemental data yielded a model accounting for 62% of the variance ($R^2=0.62$, Table 7.5). Early in the season blue and green reflectances were used in the best stepwise regressions. In late July reflectance in blue, green, red, and near infrared was used. Near infrared measurements were useful before 1 July. NDVI was useful during the spring and the July-November periods. 2) Addition of supplemental data on fire history, and grazing history to a multiple image analysis was not worth its cost; information on fire and grazing treatment were of no use and inclusion of topography data increased R^2 from 0.61 to 0.63 (Table 7.5).

Measuring Fuel Loads

Models for estimating fuel loads were made by regressing reflectance against two separate estimates of fuel load. First, a minimal estimate of autumn fuel load is litter plus end-of -season standing crop. Second, a maximal estimate is litter plus spring standing dead plus end-of -season standing crop. The maximal estimate is excessive (because little graying material from the previous year is left at the end of the season), but it sets an upper limit on fuel availability.

Minimal Estimate

Assuming that most standing dead vanishes by mid-summer, we estimated total fuel using only the five spectral bands. Predictability (% of variation) was low in all periods. Using a single image, the highest R^2 were found in early spring ($R^2=0.23$), late June ($R^2=0.30$), and fall ($R^2=0.21$) (Table 7.6).

Table 7.2. Regressions predicting litter (g/m^2) from reflectance (Landsat wavebands) in each of six periods, with or without supplemental data. Variance accounted for is presented with R^2 and standard error (SE).

Litter vs spectral bands only										
Period ¹	Int ²	Blue ³	Green	Red	NIR	IR	NDVI		Adj.R ²	SE
4/25-5/30	112			-42	5		-1766		0.155	154.9
6/1-6/15	154	81	-67		5				0.006	159.1
6/15-7/1	988	127		-124	10	-8	-1099		0.131	160.4
7/1-7/20	-63	189				-84			0.061	160.5
7/20-8/10	-229					5	387		0.072	155.3
8/10-11/1	128	43		-29	9	-2			0.095	154.6

Litter vs spectral bands & supplemental data												
Period	Int	Blue	Green	Red	NIR	IR	NDVI	Topo ⁴	Graz ⁵	Fire ⁶	Adj.R ²	SE
4/20-5/30	114			-56	46	2	-1388	-47	110	2	0.431	127.1
6/1-6/15	119	69	-57		4			-43	106	2	0.403	123.3
6/15-7/1	-109				8				111	2	0.429	129.9
7/1-7/20	-374	74					331	-36	107	2	0.407	126.8
7/20-8/1	-572			38			704		107	1	0.434	121.3
8/10-11/1	104	31	12	-26	4	-2		-45	101	2	0.459	119.6

1. Time period in which the measurements were made.
2. Intercept of the regression.
3. The body of the table displays the significant coefficients for each spectral band used in the best stepwise multiple regression. The column names are blue, green, red, NIR (near infrared), IR (Infrared), and NDVI (Normalized Difference Vegetation Index).
4. Topo is the position on the slope (near pothole, mid slope, and ridgetop).
5. Graz is the abbreviation for the level of biomass component removal (standing dead removed, standing dead and soil litter removed, and the control plot).
6. Fire 'status' indicates the number of years since the site was last burned.

Table 7.3. Regressions predicting litter (g/m^2) from reflectance (Landsat bands) in six periods combined, without (left columns) or with (right columns) supplemental data. Each part of the table represents the best stepwise multiple regression for the factors listed in the table. Variance accounted for is presented with R^2 and standard error (SE).

Litter vs spectral bands ¹			Litter vs bands ¹ & supplemental factors ²		
FACTOR	COEFFICIENT	P-VALUE	FACTOR	COEFFICIENT	P-VALUE
Constant	-154	0.533	Constant	-170	0.006
Red1	-40	0.059	Red1	-50	0.004
NIR1	50	0.001	NIR1	43	0.001
NDVI1	-1921	0.001	NDVI1	-1641	0.001
Green2	-92	0.001	Green2	-112	0.001
Red2	96	0.001	Red2	109	0.001
NIR2	-10	0.063	NIR2	-7	0.102
NDVI2	1067	0.004	NDVI2	1075	0.001
NIR3	8	0.001	NIR3	8	0.001
IR3	-8	0.032	IR3	-7	0.001
Red5	---	-----	Red5	31	0.024
NDVI5	224	0.101	NDVI5	654	0.101
Blue6	41	0.048	Blue6	41	0.048
Green6	17	0.002	Green6	-----	-----
Red6	-48	0.001	Red6	-25	0.001
NIR6	7	0.020	NIR6	5	0.064
NDVI6	-1085	0.001	NDVI6	-821	0.001
			Graz	96	0.001
			Fire	2	0.001
Adjusted $R^2=0.404$ Std error=130.0			Adjusted $R^2=0.605$ Std error=105.9		

¹Numbers following spectral predictors indicate the period in which useful measurements. Period 1=April 20-May 30. 2=June 1-June 15, 3=June 15-July 1, 4=July 1-July 20, 5=July 20-Aug. 10, and 6=Aug 10-Nov 1.

² The site factors used in the regressions were topographic position on the hill (Topo), grazing history (Graz), and number of years since the site was last burned (Fire).

Table 7.4. Regressions predicting end-of-season standing crop (g/m^2) from reflectance (Landsat wavebands) in one of six periods, with or without supplemental data. Variance accounted for is presented with R^2 and standard error (SE).

Standing crop vs spectral bands only									
Period ¹	Int ²	Blue ³	Green	Red	NIR	Infra	NDVI	Adj.R ²	SE
4/25-5/30	305	-78		31	12		-701	0.335	67.9
6/1-6/15	-11	46		-35	6	3		0.293	64.5
6/15-7/1	108			-15	5			0.474	58.5
7/1-7/20	108		-6		6			0.383	54.4
7/20-8/10	114			-10	6			0.374	54.8
8/10-11/1	48			9		-2	531	0.435	59.3

Standing crop vs spectral bands & other factors											
Period	Int	Blue	Green	Red	NIR	Infra	NDVI	Topo ⁴	Graz ⁵	Fire ⁶	Adj.R ² STD ERR
4/25-5/30	339	-36			14		-692	-47			0.429 62.9
6/1-6/15	58	46		-38	4	2		-38			0.431 57.8
6/15-7/1	528			-35	7	-4	-399		-1		0.509 56.5
7/1-7/20	232	-43			3			-24			0.342 90.8
7/20-8/10	108		-10		6						0.383 54.4
8/10-11/1	119			6		-2	378	-29		-1	0.486 56.6

1. Time period in which the measurements were made.

2. Intercept of the regression.

3. The body of the table displays the significant coefficients for each spectral band used in the best stepwise multiple regression. The column names are blue, green, red, NIR (near infrared), IR (Infrared), and NDVI (Normalized Difference Vegetation Index).

4. Topo is the position on the slope (near pothole, mid slope, and ridgetop).

5. Graz is the abbreviation for the level of biomass component removal (standing dead removed, standing dead and soil litter removed, and the control plot).

6. Fire 'status' indicates the number of years since the site was last burned.

Adding data on site factors to single period image data such as topographic position, fire history, and grazing intensity improved prediction 21% (51-30)(Table 7.6). R squares increased from a maximum of 0.303 obtained in late June without the site factors to a maximum of 0.507 when site factors were included. Grazing level was significant in all models. Topography was significant in the two earliest periods, the

early July period, and the fall period. Time since the last fire was a significant predictor in most time periods.

Using reflectance measurements from all time periods as separate predictors increased the variation accounted for by about 20% (50-30) over single image measurements (Table 7.7). Blue, green, and red were used for two time periods each (Table 7.7). Near infrared was used by the best regression from early spring, early June, and the fall period. NDVI was useful from every time period except late June.

Maximal Fuel Estimate

Next, we performed this identical analysis assuming that total fuel is equal to current years production plus ground litter plus standing dead. Our results were not consistently different from the previous analysis. The previous results using the fuel variable without standing dead included were slightly better for all time periods (Table 7.6 & 7.8). Models that included the site factors were approximately 10% better when total fuel included standing dead. Models that incorporated all time period measurements in the calculation were very similar. R squared values were 0.502 when using only reflectance measurements for the model without standing dead compared to 0.525 for models using standing dead in the calculation (Table 7.7 & 7.9). When site characteristics were added these same models gave r square values of 0.683 and 0.725.

Maximal Versus Minimal

First, maximal fuel estimates and minimal fuel estimates gave similar predictions in multiple image models. R squared values were 0.502 when reflectance alone is regressed against the minimal fuel estimate versus R^2 of 0.525 against the maximal fuel estimate (Table 7.7 & 7.9). Second, using both multiple images and site data (topographic position, fire history, and grazing intensity) improved the model. R square values rose to 0.683 for the minimal estimate and 0.725 for the maximal estimate of fuel. All three site data factors were significant in models of either fuel estimation method (Table 7.7 & 7.9).

Table 7.5. Regressions predicting autumn standing crop (g/m^2) from reflectance (Landsat bands) in six periods combined, without (left column) and with (right column) supplemental data. Each part of the table presents the best stepwise multiple regression using the factors listed. The explanatory power of the regression is indicated by its R^2 and standard error (SE).

Standing Crop-Color Bands ¹			Standing Crop-Color Bands ¹ & Other Factors ²		
FACTOR	COEFFICIENT	P-VALUE	FACTOR	COEFFICIENT	P-VALUE
Constant	-238	0.088	Constant	-99	0.470
Blue1	-29	0.003	Blue1	-27	0.005
NIR1	9	0.014	NIR1	9	0.020
NDVI1	-608	0.001	NDVI1	-499	0.004
Blue2	47	0.003	Blue2	70	0.001
Green2	-38	0.006	Green2	-56	0.001
NIR2	2	0.113	NIR2	3	0.022
NDVI2	1067	0.004	----	----	----
Green3	-11	0.100	----	----	----
NIR3	5	0.001	NIR3	4	0.001
----	----	----	Blue4	-57	0.035
----	----	----	Red4	25	0.146
NDVI4	174	0.002	NDVI4	160	0.045
Green5	-37	0.04	----	----	----
Red5	39	0.016	Red5	39	0.016
NIR5	3	0.027	----	----	----
NDVI5	224	0.011	NDVI5	209	0.111
Green6	5	0.004	Green6	4	0.010
Red6	-4	0.042	Red6	-4	0.036
NDVI6	-231	0.001	NDVI6	-206	0.001
			Topo	-18	0.054
Adjusted $R^2=0.620$ Std error=51.3			Adjusted $R^2=0.625$ Std error=51.0		

¹ Numbers behind spectral predictors indicate the time periods in which useful measurements were taken. Period 1=April 20-May 30. 2=June 1-June 15, 3=June 15-July 1, 4=July 1-July 20, 5=July 20-Aug. 10, and 6=Aug 10-Nov 1.

² The site factors used in the regressions are topographic position on the hill (Topo), grazing history (Graz), and number of years since the site was last burned (Fire).

Table 7.6. Regressions predicting Fuel I (g/m^2) from reflectance (Landsat bands) in one of six periods, with or without supplemental data. Fuel I is the sum of litter and autumn standing crop. The explanatory power of the regressions is presented with R^2 and standard error (SE).

Fuel vs spectral bands only										
Time ¹	Int ²	Blue ³	Green	Red	NIR	IR	NDVI		Adj.R ²	SE
4/25-5/30	324	-68			48		-2008		0.225	186.6
6/1-6/15	183				6				0.043	186.6
6/15-7/1	1181	92		-154	15		-1211		0.303	175.1
7/1-7/20	98				7				0.124	200.3
7/20-8/10	-277					6	731		0.199	168.0
8/10-11/1	-225				6	-4	558		0.208	173.9

Fuel vs spectral bands & other factors												
Time	Int	Blue	Green	Red	NIR	Infra	NDVI	Topo ⁴	Graz ⁵	Fire ⁶	Adj.R ²	SE
4/20-5/30	436			-85	66	2	-2160	-112	117	2	0.462	156.6
6/1-6/15	184				5			-79	107	2	0.401	147.6
6/15-7/1	137				13	-9			118		0.507	147.3
7/1-7/20	-168		31				386	-67	121	2	0.409	164.5
7/20-8/10	-808			58			1225		109	3	0.468	136.9
8/10-11/1	412		11	-16	7	-3		-78	105	2	0.477	141.4

1. Time period in which the measurements were made.

2. Intercept of the regression.

3. The body of the table displays the significant coefficients for each spectral band used in the best stepwise multiple regression. The column names are blue, green, red, NIR (near infrared), IR (Infrared), and NDVI (Normalized Difference Vegetation Index).

4. Topo is the position on the slope (near pothole, mid slope, and ridgetop).

5. Graz is the abbreviation for the level of biomass component removal (standing dead removed, standing dead and soil litter removed, and the control plot).

6. Fire 'status' indicates the number of years since the site was last burned.

Table 7.7. Regressions predicting Fuel I (g/m^2) from reflectance (Landsat bands) in six periods combined, without (left columns) or with (right columns) supplemental data. Fuel I is the sum of litter and end-of-season standing crop. The predictive power of the regressions is presented with R^2 and standard error (SE).

Fuel-Color Bands ¹			Fuel-Color Bands ¹ & Other Factors ²		
FACTOR	COEFFICIENT	P-VALUE	FACTOR	COEFFICIENT	P-VALUE
Constant	-848	0.011	Constant	-1039	0.002
Red1	-----	-----	Red1	-74	0.001
NIR1	28	0.001	NIR1	57	0.001
NIFRA1	-3	0.023	NIFRA1	2	0.123
NDVI1	-1491	0.001	NDVI1	-2057	0.001
Green2	-179	0.001	Green2	-153	0.001
Red2	135	0.001	Red2	117	0.001
INFRA2	---	----	INFRA2	5	0.046
NDVI2	671	0.004	NDVI2	751	0.002
NIR3	11	0.001	NIR3	11	0.001
NDVI4	342	0.051	NDVI4	241	0.068
Blue5	104	0.002	Blue5	104	0.002
Red5	----	-----	Red5	71	0.001
NDVI5	863	0.001	NDVI5	1115	0.001
Blue6	53	0.046	Blue6	----	-----
Green6	20	0.003	Green6	22	0.001
Red6	-57	0.001	Red6	-28	0.001
NIR6	7	0.069	NIR6	4	0.144
NDVI6	-1121	0.001	NDVI6	-1058	0.001
			Topo	-45	0.047
			Graz	111	0.001
			Fire	2	0.001
Adjusted $R^2=0.502$ Std error=166.7			Adjusted $R^2=0.683$ Std error=120.1		

¹ Numbers behind predictors indicate the period in which useful spectral measurements were taken.

Period 1=April 20-May 30. 2=June 1-June 15, 3=June 15-July 1, 4=July 1-July 20, 5=July 20-Aug. 10, and 6=Aug 10-Nov 1.

² Supplemental site factors used in the regressions are topographic position on the hill (Topo), grazing history (Graz), and number of years since the site was last burned (Fire).

Table 7.8. Regressions predicting Fuel II (g/m^2) from reflectance (Landsat bands) in one of six periods, with or without supplemental data. Fuel II is litter + spring standing dead + autumn standing crop. The explanatory power of the regressions is presented with R^2 and standard error (SE).

Fuel vs spectral bands only											
Period ²	Int	Blue	Green	Red	NIR	Infra	NDVI			Adj.R ²	SE
4/25-5/30	268	-53			46		-1917			0.223	208.2
6/1-6/15	214				6					0.031	211.4
6/15-7/1	179			-34	12					0.262	200.0
7/1-7/20	108				8					0.111	229.9
7/20-8/10	-302				6		816			0.188	193.5
8/10-11/1	245				6	-4	638			0.186	200.0

Fuel vs spectral bands & other factors												
Period	Int	Blue	Green	Red	NIR	Infra	NDVI	Topo ⁴	Graz ⁵	Fire ⁶	Adj.R ²	SE
4/20-5/30	478			-75	59	2	-2004	-117	155	2	0.514	164.8
6/1-6/15	212				5			-85	148	2	0.479	155.1
6/15-7/1	140				14	-9			159		0.571	152.5
7/1-7/20	-176		30				442	-71	164	2	0.475	176.7
7/20-8/10	-864			61			1336		154	2	0.560	142.4
8/10-11/1	267	33	11	-22	5	-4	346	-82	147	2	0.560	147.0

1. Time period in which the measurements were made: month/day

2. Intercept of the regression.

3. The body of the table displays the significant coefficients for each spectral band used in the best stepwise multiple regression. The column names are blue, green, red, NIR (near infrared), IR (Infrared), and NDVI (Normalized Difference Vegetation Index).

4. Topo is the position on the slope (near pothole, mid slope, and ridgetop).

5. Graz is the abbreviation for the level of biomass component removal (standing dead removed, standing dead and soil litter removed, and the control plot).

6. Fire 'status' indicates the number of years since the site was last burned.

Table 7.9. Regressions predicting Fuel II (g/m^2) from reflectance on six dates combined, without (left columns) or with (right columns) supplemental data. Fuel II is the sum of litter, spring standing crop and autumn standing crop. The predictive power of the regression is presented with R^2 and standard error (SE).

Fuel-Color Bands ¹			Fuel-Color Bands ¹ & Other Factors ²		
FACTOR	COEFFICIENT	P-VALUE	FACTOR	COEFFICIENT	P-VALUE
Constant	-790	0.009	Constant	-1174	0.001
Red1	-52	0.028	Red1	-59	0.001
NIR1	58	0.001	NIR1	47	0.001
NDVI1	-2259	0.001	NDVI1	-1914	0.001
Green2	-154	0.001	Green2	-179	0.001
Red2	117	0.001	Red2	136	0.001
INFRA2	-----	-----	INFRA2	6	0.017
NDVI2	580	0.001	NDVI2	875	0.001
NIR3	11	0.001	NIR3	11	0.001
NDVI4	284	0.067	NDVI4	264	0.052
Blue5	105	0.001	Blue5	-----	-----
Red5	-----	-----	Red5	79	0.001
NDVI5	890	0.001	NDVI5	1256	0.001
Blue6	38	0.103	Blue6	-----	-----
Green6	17	0.004	Green6	22	0.001
Red6	-47	0.001	Red6	-30	0.001
NIR6	7	0.046	NIR6	4	0.147
NDVI6	-1153	0.001	NDVI6	-1030	0.001
			Topo	-35	0.123
			Graz	146	0.001
			Fire	2	0.001
Adjusted $R^2=0.524$ Std error=147.1			Adjusted $R^2=0.725$ Std error=123.9		

¹ Numbers behind spectral predictors indicate the period in which useful measurements were taken.

Period 1=April 20-May 30. 2=June 1-June 15, 3=June 15-July 1, 4=July 1-July 20, 5=July 20-Aug. 10, & 6=Aug 10-Nov 1.

² The supplemental site factors used in the regressions are topographic position on the hill (Topo) Grazing history (Graz), and number of years since the site was last burned (Fire).

Model Validation

We validated our best regressions for the biomass components by randomly splitting our data into equally-sized data sets. We ran best stepwise regression on one-half of the data for each biomass component. Using these results we predicted the component for the other half of the data. Validation was tested using paired t-tests.

All components of biomass were predicted very well using predictions from one-half of the data for the predictions. The measured average end-of-season standing crop averaged 208 g/m² compared to 196 g/m² with a difference of 11.6 g/m² (92.3 sd). The two end-of-season estimates were not significantly different ($t=1.168$, 85df, $p=0.24$). Litter predictions were even better. The measured litter values averaged 138 g/m² compared to our predicted litter estimations of 136 g/m². The average difference was only 2.8 (191sd). This difference was not significantly different ($t=0.133$, 85 df, $p=0.89$). The spring fuel estimates were also not significantly different from each other ($t=-0.976$, 85df, $p=0.33$). Fall fuel predictions were also similar to measured values ($t=-0.809$, 85df, $p=0.42$).

Discussion

Our capacity to estimate standing crop from Landsat wavebands acquired in any one period was disappointing. For litter, end-of-season standing crop, and total fuel, the highest R^2 were 0.16 (May), 0.44 (Sept), and 0.23 (May), respectively. While the estimates tended to be best in spring and fall (Tables 7.2, 7.4, and 7.6) the trends were insufficient to encourage data (image) acquisition in one season over another. Our ground based reflectance data may estimate biomasses better than data gathered from a remote measurement instrument. Others have had difficulty predicting biomass from reflectance data (eg litter, van Leeuwen and Huete 1995) and attribute the difficulty to confounding effects of wet and dry soils.

We tested two mechanisms for improving these simple (conventional) estimates. The first was inclusion of additional site/field data possibly available to the manager, that is, topography, fire history, and grazing history. Using these data, the best R^2 for litter, end-of-season standing crop, and total fuel increased to 0.45 (September), 0.51 (June), and 0.51 (June, Tables 7.2, 7.4, and 7.6). We separately consider what underlies the biomass predicting power of these data. 1) It is not surprising that fire history

contributed to explanation of litter abundance and fuel load, but not to end-of-season standing crop. One expects litter load to increase with time since fire, though the correlation is imperfect (Table 7.1). Fuel load will be influenced by litter load, because litter is a fuel component. However, total current end-of-year standing crop measured on our sites was unaffected by fire history, because yield on long unburned and recently burned sites did not differ; this is generally observed, except where high yields are associated with especially large pre-fire litter loads (Weaver & Rowland 1952; Penfound 1964; Hulbert 1988). Since it is predictive and likely available to a land manager, fire history is worth including in an analysis of fuel loads.

2) Our simulated grazing treatment contributed to estimation of litter, end-of-season standing crop, and total fuel (Tables 7.2, 7.4, and 7.6). Our treatments were no removal, standing dead removal, and standing dead and litter removal, roughly approximating moderate and heavy grazing as it affects the fuel accumulation (Aldous 1930; Penfound 1964; Hulbert 1988; Risser 1985). Because the plots differed greatly in amounts of litter (Table 7.1) and did not differ in productivity (Table 7.1) the 'grazing response' recorded is due to differences in litter—contributing directly or as a correlate of standing crop. 3)

Topography affected all three biomass components in the same four of six periods (Table 7.2, 7.4, and 7.6). The topographic input was expected because sites become more productive as one moves down from hilltop to slope to bottom. Given the strength of this correlation, the a-seasonal (non consecutive) dispersion of affected and unaffected periods is surprising. Perhaps a reflectance component out-predicts topography (removes it from the equation) in certain periods, perhaps dry ones.

The second device for improving biomass estimates is combining information from multiple (six) separate images. R^2 for litter, end-of-season standing crop, and total fuel were 0.40, 0.62, and 0.68 (Tables 7.3, 6.5, and 7.7). Further improvement of R^2 by inclusion of more reflectance data is practically unattainable, due both to lack of funds and difficulty of scheduling so much sampling, except through Landsat. Can one combine supplementary data and multiple images? Such combination improved our litter estimate ($R^2=0.61$), but had little effect on our estimates of end-of-season standing crop ($R^2=0.63$) and total fuel ($R^2=0.68$).

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