BISON (*BISON BISON*) FECAL PATS AS A SMALL-SCALE DISTURBANCE ON TALLGRASS PRAIRIE

By

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NOMENCLATURE

DC	Duration of fecal pat combustion from ignition to exhaustion
FH_{adj}	Adjusted low heat of combustion for fecal pats
FD	Flame depth of the head fire
FL	Flame length of the head fire
FW	Fecal fuel consumed in kg/m^2
H	Low heat of combustion for fine fuel = 15, 830 kJ/kg
HA	Heat per unit area given in kJ/m^2
H_{adj}	Adjusted low heat of combustion for fine fuel
HH	High heat of combustion determined by bomb calorimetry
HH_{adj}	High heat of combustion adjusted for the vaporization of water
I_B	Byram's fireline intensity in kJ/m^2
I_R	Fire reaction intensity $kJ/m^2/sec$, or kW/m^2
R	Rate of spread of the flame front for fine fuel
W	Fine fuel consumed in kg/m^2

CHAPTER I

INTRODUCTION

This thesis is composed of two distinct manuscripts formatted for submission. Chapter II is formatted for the *Journal of Vegetation Science* and Chapter III is formatted for the *American Midland Naturalist*. Each manuscript is complete as written and requires no additional material for support. Manuscripts are arranged in order of text, literature cited, tables and figures.

CHAPTER II

DISTURBANCE ASPECTS OF BISON (*BISON BISON*) FECAL PATS WITHIN A TALLGRASS PRAIRIE INFLUENCED BY FIRE AND BISON GRAZING

Abstract. Bison grazing and fire are landscape-scale disturbances that can interact spatially and temporally to influence plant species abundance, diversity, and spatial patterning in tallgrass prairie. We hypothesized how the model of bison grazing×fire interaction within tallgrass prairie may be influenced at scales smaller than the landscape by interactions with bison fecal pats. We focused our study on three forb species as indicators of disturbance. To examine the disturbance associated with bison fecal pats, we investigated the mid- (100 m^2) and small-scale (< 0.5 m^2) influence of the presence of unburned and burned bison fecal pats on forb abundance within different burn patches on tallgrass prairie. Patches varied in disturbance intensity created by bison grazing and timing of fire. Forb abundance differed among burn patches, but we found little evidence of a relationship between fecal pat density and forb spatial patterns at either the mid- or small-scale. Our results indicate that bison fecal pats and bison grazing, unlike cattle fecal pats and cattle grazing, do not interact to create a substantial disturbance to tallgrass prairie vegetation.

Keywords: Burn season; Disturbance interactions; Spatial scale.

Nomenclature: The Great Plains Flora Association (1986).

Introduction

The tallgrass prairie of Central North America evolved under the influence of frequent disturbance by fire and bison (*Bison bison*) (England & DeVos 1969; Adams et al. 1982; Axelrod 1985). Bison grazing×fire interactions are important influences on diversity and spatial patterns of vegetation in grassland systems (Vinton et al. 1993; Hartnett et al. 1996). Burning generally favors tallgrasses, and bison may heavily graze recently burned areas because of the high quality regrowth after a fire (Coppock & Detling 1986; Shaw & Carter 1990). Intense grazing of burned patches defers grazing on unburned patches, which results in an accumulation of fuel and an increased probability of fire in unburned patches (Steuter 1986; Hobbs et al. 1991). Therefore, fire alters bison grazing activity and bison grazing determines the extent and intensity of fires, resulting in an interaction of disturbances that produces a dynamic patch mosaic of plant communities within a grassland (Steuter et al. 1995; Hamilton 1996). The bison grazing×fire interaction model is complicated by season of the burn which influences the effects of fire (Ewing & Engle 1988; Biondini et al. 1989; Howe 1994a) and bison preference for certain patches (Shaw & Carter 1990).

The importance of large-scale (> 1-ha) disturbances in grasslands has been well documented (Anderson 1982; Wright & Bailey 1982; Gibson 1989; Glenn et al. 1992; Vinton et al. 1993). Also important are the numerous small-scale (< 0.5-m^2) disturbances that influence plant species diversity and spatial patterning by allowing certain non-matrix plant species to compete for resources (Coffin & Lauenroth, 1988 and 1989; Gibson 1989; Gibson et al. 1993). Forb-dominated patches within grassland systems are often associated with intense small-scale disturbances (Hobbs & Mooney 1985), and abundant small-scale disturbances within a landscape, can have a cumulative regional influence (Parish & Turkington 1990; Glenn et al. 1992).

A cattle (*Bos taurus*) fecal pat represents a small-scale disturbance agent that can directly and indirectly influence spatial patterns in vegetation. Vegetation within 30 cm of the edge of a cattle fecal pat can be directly influenced by nutrients leached from the fecal material for up to three months after deposition (Norman & Green 1958; MacDiarmid & Watkin 1971). Cattle fecal pats indirectly influence surrounding vegetation by altering grazing activity, since cattle avoid grazing near fecal pats for several months, depending on the availability of uncontaminated forage (Castle & MacDaid 1972; Forbes & Hodgson 1985). To our knowledge, no published research has examined the direct or indirect small-scale influence of bison fecal pats on vegetation within tallgrass prairie or whether or not bison fecal pats interact with larger-scale disturbances. If bison fecal pats represent a small-scale disturbance under the influence of bison grazing in the same manner as cattle fecal pats represent a small-scale disturbance under the influence of cattle grazing, a high density of bison fecal pats may modify the larger-scale influence of the bison grazing×fire interaction.

The disturbance of fecal pats in the bison grazing×fire interaction model may increase when fecal pats combust in subsequent fire events. A fecal pat represents a patch of concentrated fuel on the grassland landscape. Dry fecal pats consumed in a grassland fire can produce heat that may increase the disturbance intensity and influence small-scale spatial patterning of plant species.

Whether benefiting from grazing protection, added nutrients, or reduced competition from grasses, certain forb species may flourish where bison fecal pats are abundant. To investigate the interacting disturbances of bison grazing, fire, and fecal pats on tallgrass prairie, we examined mid-scale (100-m^2) and small-scale ($< 0.5\text{-m}^2$) patterns of forb abundance and fecal pat density within an array of disturbance patches created by fire and bison grazing.

Methods

Study Area

We conducted our study on The Nature Conservancy's Tallgrass Prairie Preserve, located in the Osage Hills of northeastern Oklahoma (36°49'N, 96°23'W) along the Oklahoma-Kansas border (Hamilton 1996). The preserve includes almost 15,000 ha of unplowed tallgrass prairie that was previously used as a cattle operation. All data were collected within the 2,250 ha bison enclosure. A herd of about 450 bison of mixed sex and age inhabited the enclosure since 1993. The soils were all Loamy-prairie or Loamy-prairie Complex (USDA-SCS 1992). Vegetation within the preserve is dominated by tallgrasses including *Andropogon gerardii, A. scoparius, Sorghastrum nutans,* and *Panicum virgatum* (USDA-SCS 1992) with forb density varying among areas of different disturbance intensities created by bison grazing and fire.

Prescribed burning for the preserve consists of 80% dormant season and 20% growing season burns conducted randomly throughout the enclosure in a regime designed to mimic pre-European settlement burn frequency and season. Burns are conducted on patches of varying size under a variety of fuel and weather conditions with an approximate five year return interval (Hamilton 1996). In keeping with the bison grazing×fire interaction model, bison movement and selective grazing were unrestricted. We selected four patches studied by Coppedge (1996) on which to examine mid- and small-scale influences of bison fecal pats. Bison are attracted to recently burned areas and tend to heavily graze the fresh regrowth following burning (Shaw & Carter 1990; Coppedge 1996). Because bison utilize burned areas extensively during the first month of regrowth and decrease use with increasing time since burning (M. Biondini pers. comm.), we classified the recently burned, heavily grazed patch as the most intensely disturbed. The patch that had not been burned in over two years with little or no current year's bison use was classified as the lowest level of disturbance, with intermediate disturbance levels represented by the two remaining patches. On three other patches, we studied the small-scale influence of burned bison fecal pats.

Indicator Species

All vegetation data were recorded from late July to early August during the 1995 and 1996 growing seasons. Because forbs contribute substantially more to plant diversity than grasses in tallgrass prairie (Howe 1994b; Collins & Glenn 1995), we focused our research on three forb species, *Ambrosia spp., Gutierrezia dracunculoides,* and *Vernonia spp.*, as indicators of disturbance (Fahnestock & Knapp 1993; Vinton et al. 1993; Hartnett et al. 1996). Both *A. psilostachya*, a perennial species, and *A. artemisifolia*, an annual species, were present on all burn plots, but immature shoots were not easily identified in the field so the two species were combined into a single category. *A. psilostachya* dominated in every case. Likewise, *V. baldwinii* and *V. arkansana* were both present, but were difficult to identify in the immature stage and were combined. *V. baldwinii* dominated in every case.

All sampling was conducted within 1-ha macroplots that we established on four different patches within the bison enclosure that exhibited different levels of disturbance intensity. Each macroplot was laid out in a 100 × 100-m grid and was sectioned into one hundred 100-m^2 (10 × 10 m) microplots. We oriented the macroplots north to south and each microplot was numbered northing and easting.

Mid- and Small-scale Influence of Bison Fecal Pats

We examined mid-scale influences of fecal pats by comparing the density of fecal pats with forb canopy cover within each 100-m^2 microplot. We estimated fecal pat density by counting fecal pats within a 78.5-m^2 circular plot in the center of each microplot. Canopy cover of the three forbs *Ambrosia spp.*, *G. dracunculoides*, and *Vernonia spp.* was determined according to Daubenmire's classifications within a rectangular 20 × 50-cm quadrat placed at ten evenly-spaced locations within the 78.5-m^2 circular quadrat in the center of each microplot (Daubenmire 1959).

To determine the small-scale influence of bison fecal pats, we measured forb stem density around fecal pats using a set of nested arched quadrats. The inner quadrat was a semicircular arch with a 30-cm radius (0.28 m^2) and was designed to represent the area of potential influence surrounding a fecal pat as described by Norman & Green (1958). The outer quadrat was also a semicircular arch with a 30-cm radius (0.53 m^2) nested exterior to the inner quadrat to represent an area presumed to have no influence. We randomly selected 30 microplots within each of the four macroplots, and we sampled the vegetation around the first large (> 15-cm diameter) fecal pat we encountered within the selected microplots. When no large fecal pats were present within the selected microplot, another microplot was chosen at random. No fecal pats were sampled twice. We measured forb density by orienting the nested arch quadrats on one side of each fecal pat and counting all forb stems within each quadrat. Stem density was recorded for *Ambrosia spp.*, *G. dracunculoides,* and *Vernonia spp.*

Small-scale Influence of Burned Bison Fecal Pats

We tested the small-scale influence of burned bison fecal pats with data collected on three additional patches burned in September and December of 1995 and April of 1996. All three burns were on upland sites that had not been burned within the previous two growing seasons. Fecal pats were deposited by the bison before the growing season of 1995. Our sampling was conducted within a 0.5-ha area near the center of the burn patches, which averaged 30 ha in size. We collected and weighed ten randomly-selected fecal pats immediately before burning. We also collected and weighed all herbaceous fuel within ten, 0.25-m^2 quadrats placed at random in the same general area that we collected the fecal pat samples. Fecal pat and fine fuel samples were oven-dried and weighed, and moisture content calculated on a dry-weight basis. Weather conditions and fecal pat and fine fuel physical properties are presented in Table 1.

We established two 5 × 50-m linear transects in each of the three burn patches. We mapped the location of 30 burned fecal pats per transect in the September and April burn patches and 15 fecal pats per transect in the December burn patch. We identified the burned fecal pats with a coded tag so each fecal pat could be relocated the following growing season. The tags were inserted into the ground at the north edge of each fecal pat and were driven flush to the soil so as not to influence bison grazing activity. The area of each mapped fecal pat was estimated by the size of the remaining ash residue following complete combustion.

We recorded vegetation data around the burned fecal pats from late July to early August 1996 using the nested arch quadrats as described for unburned fecal pats. We measured forb density by orienting the nested arch quadrats on the northward side of each fecal pat and counting forb stems within each quadrat. We recorded stem density within each quadrat for each of the three indicator forbs. We estimated forb and grass productivity by moving the nested quadrats to the southward side of the fecal pat and harvesting to ground level all current year's standing crop of grasses and forbs located within each quadrat. Forb standing crop included the standing crop of the three indicator forbs as well as all other forbs present within the quadrats. Each sample was oven dried and weighed to obtain total dry weight.

Analyses

We inspected semivariograms of the abundance of both fecal pats and forbs to determine if each were independently distributed among microplots. Both fecal pats and forbs were spatially autocorrelated. To overcome the problem of limited permutations and to correct for spatial autocorrelation, we compared mid-scale (100 m^2) spatial patterns of fecal pats and mid-scale spatial patterns of forbs using Pearson correlations in a random shifts method (Palmer & Van der Maarel 1995). We used a paired t-test to compare forb density and forb and grass standing crop between the inner and outer nested quadrats to identify the small-scale ($< 0.05\ m^2$) influence of the presence of unburned bison fecal pats on forb stem density. We also used a paired t-test to compare the inner and outer nested quadrats placed around burned bison fecal pats to determine the small-scale influence of burned fecal pats on forb stem density and forb and grass standing crop.

We used simple linear regression to model stem density of the three indicator forbs as a function of a disturbance factor. The regression equation was:

$$Y_i = \beta_0 + \beta_i X_i$$

in which Y_i is stem density of a forb indicator species within the inner nested arch quadrat. Disturbance factors (independent variables) were surface area of the fecal pat, the number of months since burning, and the interaction of surface area of the fecal pat and the number of months since burning. Number of months since burning is an index of bison grazing intensity on a burned patch representing the number of months of exposure to intense selective grazing by bison after burning, and is confounded with the season of burning (i.e. burn date). Significance of independent variables was set at $P \leq 0.05$.

Results

Forb abundance differed among burn patches, but we found little evidence of a relationship between spatial patterns of bison fecal pats and spatial patterns of forbs at the mid-scale ($100\ m^2$) even though the fecal pats were not distributed randomly. Microplots contained from 0 to 32 individual fecal pats. Patch 2, the most intensely disturbed patch, contained 1,400 fecal pats in 1996. Density of fecal pats was not associated with forb canopy cover in either 1995 or 1996 (Tables 2 and 3), nor was fecal pat density in 1995 associated with forb canopy cover in the 1996 growing season (Table 4). *Vernonia spp.* was the only exception with mid-scale (100 m^2) spatial patterns positively associated with fecal pats in Patch 2 in 1996 (Table 3). The association was weak and possibly a result of chance. The absence of an influence of unburned fecal pats on forb abundance is further demonstrated at the mid-scale in which fecal pats were non-randomly distributed among 100-m^2 microplots, but forbs were not patterned similarly.

We found little evidence that unburned fecal pats influenced forb stem density at the small-scale (< 0.5 m^2). In 1995, neither *Ambrosia spp.*, *G. dracunculoides,* nor *Vernonia spp.* were more abundant in the inner quadrat in any of the four macroplots (Figure 1). In 1996, *Ambrosia spp.* stems were more dense in the inner quadrat on Patch 13 ($P < 0.01$), but stem density in the inner quadrat differed from the outer quadrat by < 20 % (Figure 2).

We found little evidence that burned bison fecal pats influenced forb stem density at the small-scale (Figure 3). Neither *Ambrosia spp.*, *G. dracunculoides,* nor *Vernonia spp.* were more abundant in the inner quadrat in any of three burn patches. We found no differences in forb or grass standing crop around burned bison fecal pats in of three burn patches (Figure 4).

The number of months since burning was a significant independent variable in our simple linear regressions of small-scale abundance of *G. dracunculoides* and *Vernonia spp.* (Table 5). The surface area of the fecal pat at the time of burning was associated with abundance of *Ambrosia spp.* and *G. dracunculoides*, but R^2 values were low. The interaction between surface area of the fecal pat and the number of months since burning was associated with *Ambrosia spp.* and *Vernonia spp.*, but again R^2 values were low.

We must fail to reject our null hypothesis that bison fecal pats do not interact with fire and bison grazing as disturbance agents, indexed by forb abundance, in tallgrass prairie at the mid-scale. We must likewise fail to reject our null hypotheses that unburned and burned bison fecal pats represent a small-scale disturbance to tallgrass prairie. When a forb species was more abundant around burned bison fecal pats, the increase was small. Patch-level factors, season of burning and bison grazing intensity, were the overriding influences on forb abundance.

Discussion

As the bison grazing×fire interaction model predicts, forb abundance varied among patches because of differences in burn season and grazing intensity. Our results suggest that forbs benefit more from the removal of competitive grasses under bison grazing than from nutrients released from bison fecal pats. Therefore, bison grazing is a greater disturbance at the patch-scale (> 1 ha) than the disturbance of unburned or burned fecal pats at the small-scale (< 0.05 m^2).

A cattle fecal pat is a small-scale disturbance that produces a significant influence on surrounding vegetation in grasslands (Norman & Green 1958; Marsh & Campling 1970; Parish & Turkington 1990). Certain plant species benefit from nutrients leached from cattle fecal pats into the soil, increasing production in an area as great as 1.2 m from the edge of the fecal pat (Norman & Green 1958; Marsh & Campling 1970; MacDiarmid & Watkin

1971). Some plants are smothered under a cattle fecal pat, while other nearby plants are sheltered from grazing because cattle avoid areas fouled by the dung (MacDiarmid & Watkin 1971; Castle & MacDaid 1972; Forbes & Hodgson 1985). Cattle avoid grazing within an area 30 cm from the edge of a cattle fecal pat for nearly a year after the fecal pat is deposited (Norman & Green 1958; Castle & MacDaid 1972; Forbes & Hodgson 1985). The small-scale influences of cattle fecal pat disturbances on grassland vegetation may be noticeable for up to three years following deposition (Williams & Haynes 1995).

The grazing behavior of large herbivores is influenced by preferential selection of forage at the feeding station, patch, plant community, and landscape scales (Senft et al. 1987; Bailey et al. 1996). Studies on shortgrass, mixed grass, and tallgrass prairies demonstrate that bison consume a greater percentage of grasses than cattle (Van Vuren 1982 & 1984; Plumb & Dodd 1993; Coppedge 1996). Bison and cattle also differ in foraging strategy at different spatial scales, with bison selecting against patches with a relatively high forb density (Vinton et al. 1993) and with cattle grazing more selectively within a patch (Schwartz & Ellis 1981). Differences in grazing behavior lead us to expect scale-dependent differences in vegetation composition under the influence of grazing by bison and cattle.

Our results suggest that patch-level forb abundance increased under intense selective grazing by bison, and that this increase was independent of fecal pats. Other researchers have also reported that intense selective grazing by bison may result in an increase in forb abundance within a patch (Fahnestock & Knapp 1993). Because cattle graze selectively within patches and cattle are repelled by fecal pats (Castle & MacDaid 1972; Forbes & Hodgson 1985), small-scale areas within a patch will be differentially selected by cattle so that abundance of forbs at the patch-level will differ among patches of varying fecal pat density. If bison avoid grazing small-scale areas around fecal pats in the same manner as cattle (Castle & MacDaid 1972; Forbes & Hodgson 1985), the patch-level competitive advantage forbs receive from selective gramnivory by bison within the patch would be partially offset by the ungrazed grasses within 30 cm of fecal pats. If bison do not avoid grazing near fecal pats, as our results suggest, the patch-level competitive advantage for forbs may be greater under bison grazing than under cattle grazing at similar levels of herbivory.

It is possible that our chosen scales of investigation may not have corresponded with spatial or temporal patterns of forbs surrounding bison fecal pats. Some of the unburned fecal pats we sampled were old and dry and the response in surrounding vegetation may have passed before our data collection. However, bison use following burning on two patches was heavy in both 1995 and 1996, and both patches contained a higher number of fresh fecal pats than dry fecal pats, which were mostly consumed during the fires (personal observation). Even with a high density of fresh bison fecal pats, we observed very few differences in forb canopy cover or stem density at the small scale. Bison fecal pats were non-randomly distributed within a patch, which suggests a high density of fecal pats (> 15 fecal pats per 100 m^2) correspond to a ruminating area where bison congregate and rest. Increased wallowing and trampling in these areas would reduce some matrix plants in the short term providing gaps for invasion by opportunistic forbs. The result would be greater forb abundance within a patch in later growing seasons (Coppedge 1996; Hartnett et al. 1997). However, our results indicated that the non-random distribution of bison fecal pats was not associated with forb spatial patterns at the mid-scale. Therefore, bison fecal pats may serve as indicators of bison-induced disturbances at scales larger than the 100-m^2 area we investigated.

Cattle, through substantial fecal deposits, can influence plant species diversity and production at scales larger than the area immediately surrounding the fecal pat (Peterson et al. 1956; MacLusky 1960; Castle & MacDaid 1972). The area of potential influence of bison feces, calculated in the same manner MacLusky (1960) and Williams & Haynes (1995) calculated the area of influence for cattle feces, was about 400 m^2 in Patch 2. If the presence of bison fecal pats influences certain forb species in a manner we were unable to detect, this represents a potential small-scale disturbance and source of variation in plant species diversity within the bison grazing×fire interaction model.

Our results suggest bison fecal pats do not represent as great a disturbance as do cattle fecal pats. We were unable to detect any discernible pattern of association between fecal pats and forb abundance at either the mid-scale (100 m^2) or small-scale (< 0.05 m^2). With regard to the bison grazing×fire interaction model, bison fecal pats do not appear to interact with bison grazing or fire to influence tallgrass prairie vegetation, particularly forb abundance as an indicator of disturbance. The absence of a measurable response from either forbs or grasses adjacent to bison fecal pats is further evidence that bison are less selective grazers than cattle within a patch and that this difference in selection is reflected in vegetation. Because there was no change in grass production surrounding fecal pats, it appears that bison utilize all available graminoid forage within a feeding station regardless of the presence of fecal pats. This is unlike cattle, which avoid fouled areas if other forage is available. Because forbs generally increased when disturbance intensity was high, but did not increase in the presence of bison fecal pats, it appears that forbs benefit more from the removal of competitive grasses by bison grazing at the patch level than from a small-scale input of nutrients from fecal pats. We conclude that the absence of a bison grazing×fecal pat interaction highlights the different grazing strategies of bison and cattle, and that the differences between bison and cattle grazing selectivity are discernible within plant communities at various spatial scales.

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Table 1. Weather, fuel conditions, and fecal pat characteristics associated with tallgrass fires conducted within the bison unit of the Tallgrass Prairie Preserve, Osage County, Oklahoma.

Burn Date	September 1995	December 1995	April 1996
Relative humidity (%)	50	62	16
Air temperature (°C)	30	14	26
Wind speed (km/hr)	7	14	20
Fine Fuel load (kg/ha)	6,640	9,480	6,560
Fine fuel moisture (%)	72	16	6
Fecal pat:			
moisture (%)	8	37	9
mass (g)	130	60	67
density (g/cm^3)	0.22	0.23	0.21
area (cm^2)	250	270	230

Table 2. Pearson correlation coefficients expressing the degree of association between 1995 bison fecal pat density and 1995 forb stem density. Values were determined with a randomization test to correct for spatial autocorrelation within large-scale (1-ha) disturbance patches. Patches are listed from left to right in order of increasing disturbance intensity. No correlations were significant at $P < 0.025$ or $P > 0.975$.

	Disturbance Patch			
Species	Patch 2	Patch 11	Patch 13	Patch 14
Ambrosia spp.	-0.17	-0.06	-0.14	0.11
G. dracunculoides	0.14	0.11	0.05	0.12
Vernonia spp.	-0.08	-0.09	-0.20	-0.06

Table 3. Pearson correlation coefficients expressing the degree of association between 1996 bison fecal pat density and 1996 forb stem density. Values were determined with a randomization test to correct for spatial autocorrelation within large-scale (1-ha) disturbance patches. Patches are listed from left to right in order of increasing disturbance intensity. ∗ = Significance at $P < 0.025$.

	Disturbance Patch			
Species	Patch 11	Patch 13	Patch 14	Patch 2
Ambrosia spp.	-0.11	0.13	0.19	-0.05
G. dracunculoides	--	--	0.03	0.16
Vernonia spp.	-0.04	-0.11	0.08	0.22 ∗

Table 4. Pearson correlation coefficients expressing the degree of association between 1995 bison fecal pat density and 1996 forb stem density. Values were determined with a randomization test to correct for spatial autocorrelation within large-scale (1-ha) disturbance patches. Patches are listed from left to right in order of increasing disturbance intensity. No correlations were significant at $P < 0.025$ or $P > 0.975$.

	Disturbance Patch			
Species	Patch 11	Patch 13	Patch 14	Patch 2
Ambrosia spp.	-0.18	-0.14	0.21	-0.31
G. dracunculoides	0	0	0.03	0.05
Vernonia spp.	-0.03	-0.01	-0.01	0.01

Table 5. Results of regression analysis where Y = forb stem density within 30 cm of burned bison fecal pats on three different burn patches, X_1 = surface area of the fecal pat at the time of burning, and X_2 = number of months since burning.

Model	B_0	Coefficient	SE	P	R^2
Ambrosia spp.					
$Y=\beta_0+\beta_1X_1$	78.99	-0.22	0.04	< 0.01	0.15
$Y=\beta_0+\beta_1X_2$	37.49	1.06	1.53	< 0.49	0.00
$Y=\beta_0+\beta_1(X_1{*}X_2)$	63.70	-0.02	0.00	< 0.01	0.08
G. dracunculoides					
$Y=\beta_0+\beta_1X_1$	10.09	0.04	0.02	< 0.06	0.02
$Y=\beta_0+\beta_1X_2$	44.44	-3.71	0.67	< 0.01	0.17
$Y=\beta_0+\beta_1(X_1{*}X_2)$	19.48	0.00	0.00	< 0.21	0.01
Vernonia spp.					
$Y=\beta_0+\beta_1X_1$	2.30	0.00	0.01	< 0.53	0.00
$Y=\beta_0+\beta_1X_2$	-2.16	0.65	0.16	< 0.01	0.09
$Y=\beta_0+\beta_1(X_1{*}X_2)$	1.31	0.00	0.00	< 0.01	0.04

Figure 1. Forb stem density within nested arch quadrats placed around unburned bison fecal pats in 1995 in four different burn patches. Note that the scale is different for each y axis. No differences were found at the $P < 0.05$ level. Patches are ordered from left to right in order of increasing disturbance intensity.

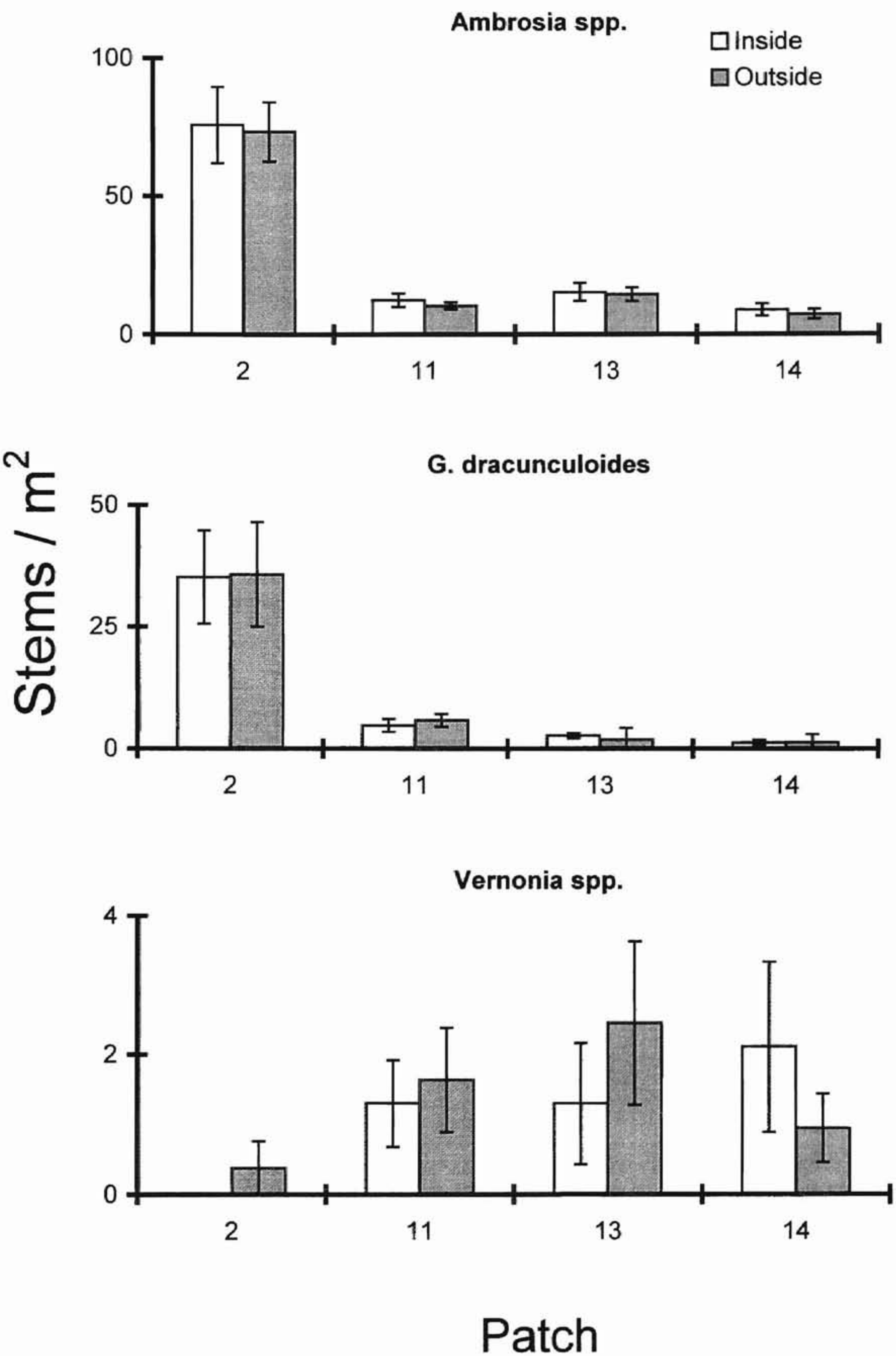

Ambrosia spp.
Inside
Outside
100
50
0
2
11
13
14
Stems / m^2
G. dracunculoides
50
25
0
2
11
13
14
Vernonia spp.
4
2
0
2
11
13
14
Patch

Figure 2. Forb stem density within nested arch quadrats placed around unburned bison fecal pats in 1996 in four different burn patches. Note that the scale is different for each y axis. Asterisk identifies a pair of means within a patch that are different at the $P < 0.05$ level. Patches are ordered from left to right in order of increasing disturbance intensity.

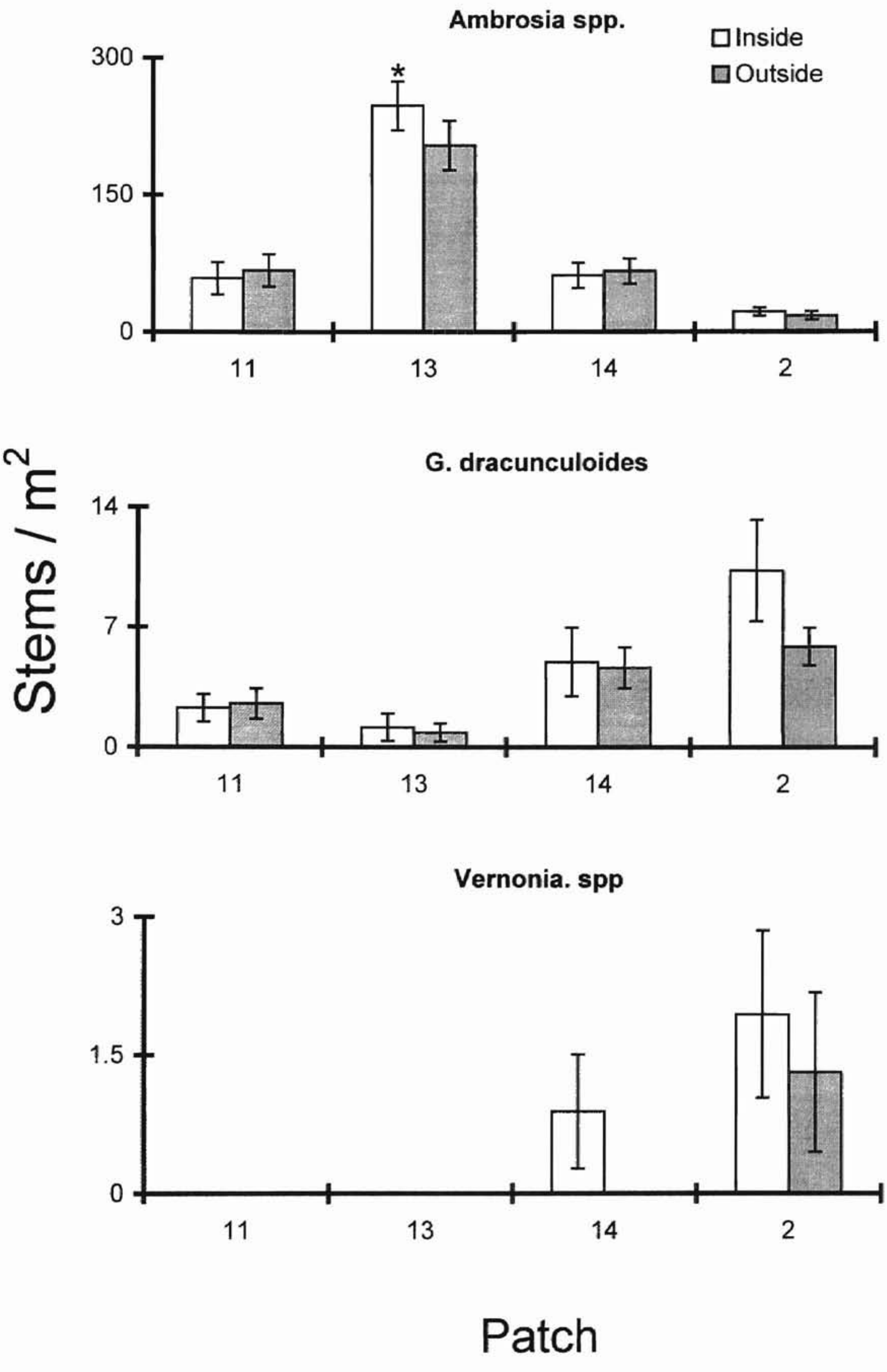

Ambrosia spp.
Inside
Outside
300
150
0
*
11
13
14
2
Stems / m^2
G. dracunculoides
14
7
0
11
13
14
2
Vernonia. spp
3
1.5
0
11
13
14
2
Patch

Figure 3. Forb stem density within nested arch quadrats placed around burned bison fecal pats in three different burn patches burned at different seasons. Note that the scale is different for each y axis. No differences were found at the $P < 0.05$ level. Patches are ordered from left to right in order of increasing disturbance intensity.

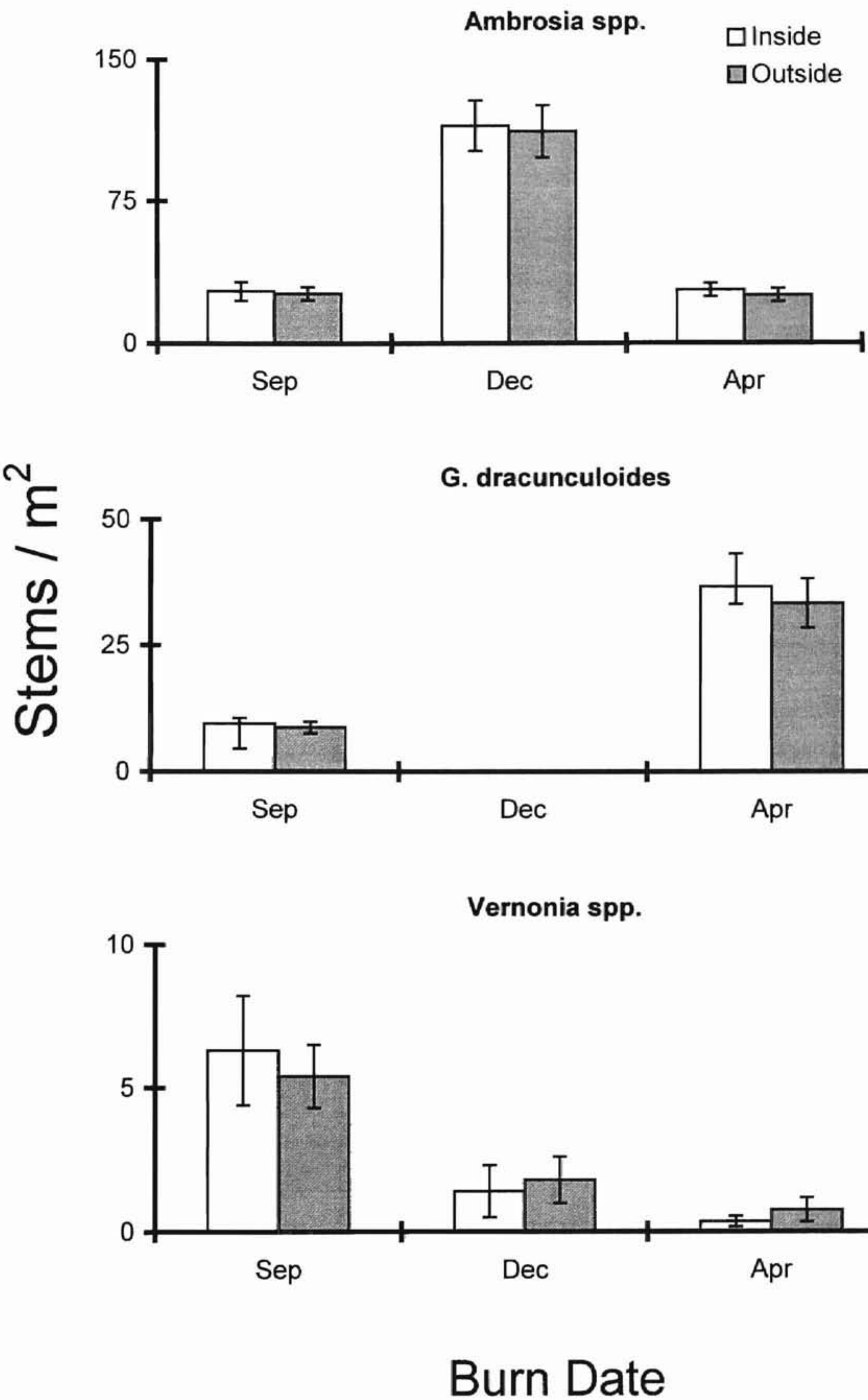
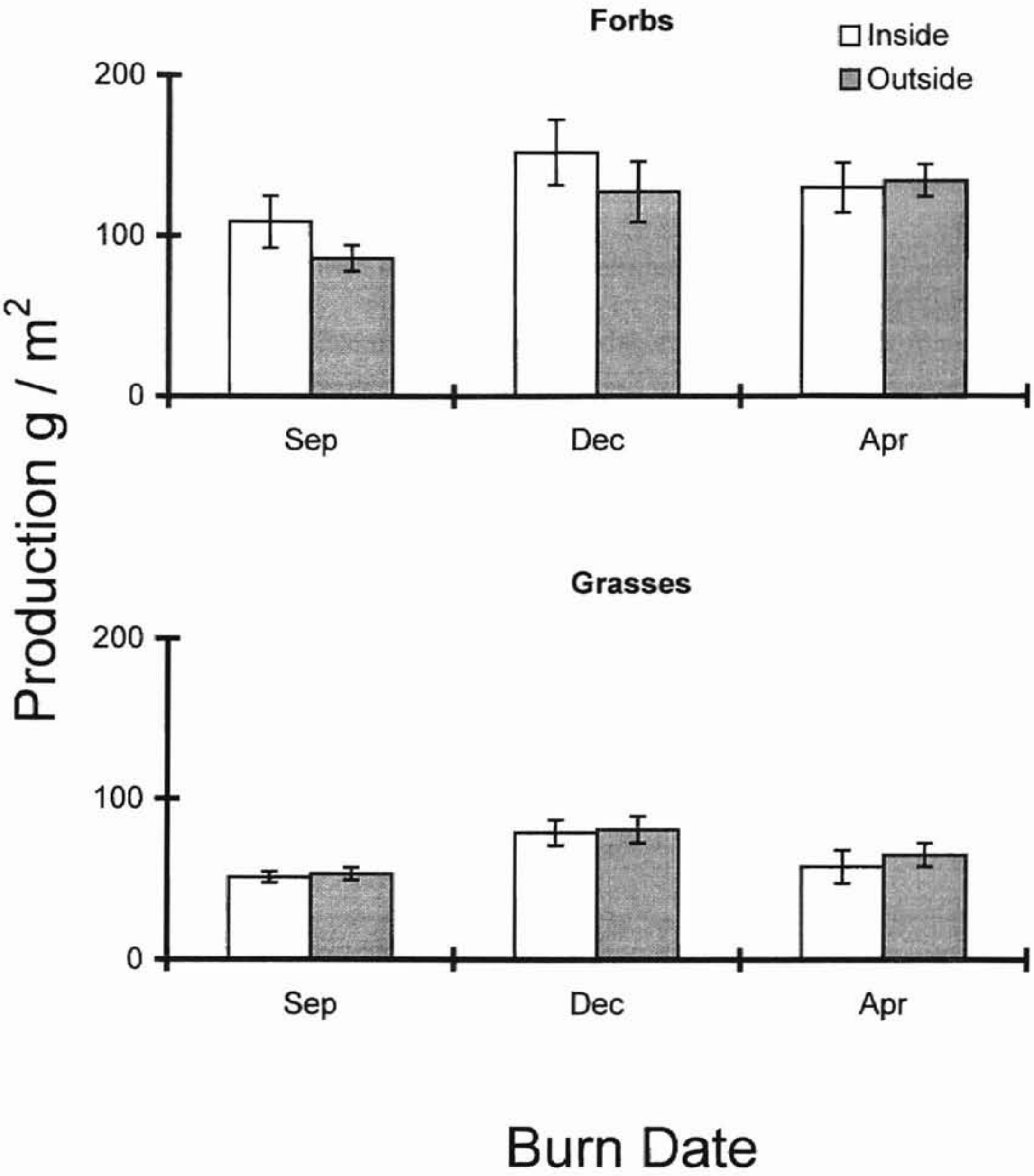

Ambrosia spp.
Inside
Outside
150
75
0
Sep
Dec
Apr
Stems / m2
G. dracunculoides
50
25
0
Sep
Dec
Apr
Vernonia spp.
10
5
0
Sep
Dec
Apr
Burn Date

Figure 4. Forb and grass standing crop within nested arch quadrats placed around burned bison fecal pats in three different burn patches burned at different seasons. No differences were found at the $P < 0.05$ level.


Forbs
Inside
Outside
200
100
0
Sep
Dec
Apr
Production g / m^2
Grasses
200
100
0
Sep
Dec
Apr
Burn Date

CHAPTER III

COMBUSTION CHARACTERISTICS OF BISON FECAL PATS IGNITED BY GRASSLAND FIRES

ABSTRACT.—We quantified the combustion characteristics of bison fecal pats following three fires conducted at different seasons on an Oklahoma tallgrass prairie. We compared heat per unit area, rate of energy consumption, and duration of combustion of fecal pats with fireline intensity, reaction intensity, and heat per unit area of fine fuels under different environmental conditions. Environmental conditions at the time of burning determined the intensity of the fire in the fine fuels as well as the consumption rates of fecal pats. We found no correlation between fine fuel fire behavior and fecal pat combustion characteristics. Density differences between fine fuels and fecal pats resulted in different fuel moisture lag times and different fire behavior for the two fuel types relative to different fire environments.

Keywords.—Byram's fireline intensity, Burn season, Keetch/Byram Drought Index (KBDI), fuel load, fire intensity, tallgrass prairie.

INTRODUCTION

The prairies of Central North America were shaped in large part by fire and grazing by large herds of American bison (*Bison bison*) (England and DeVos, 1969; Axelrod, 1985). The importance of these large-scale (> 1-ha) disturbance events to the continuation of the grasslands has been well documented (Anderson, 1982; Wright and Bailey, 1982; Gibson, 1989; Glenn *et al.*, 1992; Vinton *et al.*, 1993). Also important are the numerous small-scale (< 2-m^2) disturbances that can increase the biodiversity and spatial patterning of plant communities (Collins and Glenn, 1988; Coffin and Lauenroth, 1989; Steuter *et al.*, 1995).

Many researchers have examined the influence of large and small-scale disturbances in terms of disturbance frequency, fire intensity, fuel loading, fuel type, bison grazing pattern, and bison stocking rate (Bragg, 1982; Engle *et al.*, 1989; Shaw and Carter, 1990; Bidwell and Engle, 1991; Fahnestock and Knapp, 1993). Differences and interactions among disturbances of varying spatial scale have also been studied (Coppock *et al.*, 1983; Coppock and Detling, 1986; Coffin and Lauenroth, 1988; Biondini *et al.*, 1989; Gibson *et al.*, 1993). One small-scale aspect of bison presence within a fire-influenced ecosystem that has been overlooked in this literature is bison fecal pats, and in particular the relative intensity of the disturbance created by a burning fecal pat. Considering the importance of small-scale disturbances in maintaining species diversity, and the vast herds of bison that once roamed the Great Plains, research focused on prairie restoration, plant diversity, or vegetation dynamics should consider the influence of fecal pats on the ecosystem.

Several studies have examined the influence of cattle fecal pats on composition and regrowth of seeded grasslands (Norman and Green, 1958; MacDiarmid and Watkin, 1971; Castle and MacDaid, 1972; Parish and Turkington, 1990). To our knowledge, no such studies have been conducted on bison fecal pats. Bunting and Wright (1974) examined the ignition capabilities of cattle fecal pats under varying environmental conditions. They found that cattle fecal pats ignited easily under hot, dry conditions and could burn with sufficient intensity to start spot fires (Bunting and Wright, 1974). However, we were unable to find any study that has quantified the combustion characteristics of either bison or cattle fecal pats. To evaluate the relative intensity of the disturbance event of combustion of bison fecal pats, we quantified the energy release and heat per unit area of combusting bison fecal pats and related these combustion characteristics to the behavior of fine-fuel fires within the grassland matrix.

MATERIALS AND METHODS

Study site.—We collected our data on The Nature Conservancy's Tallgrass Prairie Preserve, located in the Osage Hills of northeastern Oklahoma (36°49'N, 96°23'W) (Hamilton, 1996). All data were collected within the 2,250 ha bison enclosure. A herd of about 450 bison of mixed sex and age inhabited the enclosure since 1993. The soils were all Loamy-prairie or Loamy-prairie Complex (USDA-SCS, 1992).

Fuels.—Patches were burned in September 1995, December 1995, and April 1996. The three burns were conducted as part of The Nature Conservancy's prescribed fire program designed to mimic a pre-European settlement burn frequency and season. Fecal pats were deposited by the bison before the growing season of 1995. All our sampling was conducted within an area less than 0.5 ha near the center of the burn patches, which averaged 30 ha in size. We collected and weighed ten randomly selected, dry fecal pats immediately before burning. We measured the long and short axis of another sixty randomly selected fecal pats and calculated an average area of soil contact for fecal pats in each burn patch. We also collected and weighed all herbaceous fuel within ten, 0.25-m^2 quadrats placed at random in the same general area that we collected the fecal pat samples. Fecal pat and fine fuel samples were oven-dried and weighed, and moisture content calculated on a dry-weight basis. We estimated the volume of collected fecal pats by placing each in a thin plastic bag, submerging in a large graduated cylinder, and measuring the displacement. Fecal pat and fine fuel physical properties are recorded in Table 1.

We collected the post-burn fuel residue in ten, randomly placed 0.25-m^2 quadrats. We calculated fuel consumed (W) by subtracting the unburned residue from pre-burn fuel load. Because the fecal material burned completely to ash, we determined the fuel consumption of fecal material (FW) for each burn patch to be the total fecal pat mass estimated from collected samples. We used the mean area of the fecal pats in each burn patch to adjust FW to kg/m^2.

Fire Environment and Fire Behavior.—We determined air temperature and relative humidity (RH) with a standard sling psychrometer and wind speed at 2 m with a totalizing anemometer. We estimated solar radiance and KBDI drought index at the time of each burn with data from the MESONET weather station located at Foraker, Oklahoma, about four miles west of the bison enclosure (Oklahoma Climatological Survey, 1996). Mean solar radiance was calculated using values recorded at fifteen minute intervals for the three hour time period including sampling and burn time. KBDI at the time of each of the three burns was calculated using daily maximum temperature and precipitation for the year before burning with the New K-B Drought Index software (Flowers, 1989). The KBDI is used in the National Fire Danger Rating System to modify the amount of dead fuel available for consumption (Burgan, 1988). It operates on a scale of 0 to 800, with 0 representing saturation of the upper layers of the soil profile and 800 representing severe water deficit. KBDI was designed to evaluate the effects on fire activity of long term drying of litter and duff (Keetch and Byram, 1968; Melton, 1989). Weather conditions and fuel loads at the time of the fires are given in Table 1.

We measured the forward rate of spread (R) of the fire front by timing its passage between two points marked with metal poles within the fuelbed. The poles were placed 5 m apart in a line perpendicular to the fire front. We visually estimated flame depth (FD) as the headfire passed the forward pole, which was ruled in 0.25-m units. The means of three sets of fire behavior measurements were used to calculate fire behavior for each burn patch.

We calculated fireline intensity with the equation $I_B = HWR$, where I_B is the rate of energy or heat release per unit time per unit length of the fire front (Byram, 1959; Alexander, 1982). We assumed fuel heat content (low heat of combustion, H) to be 15, 830 kJ/kg, which was calculated from tallgrass prairie in north central Oklahoma (Bidwell and Engle, 1992). We adjusted H for water content in the fuel by multiplying 24 times the fuel moisture percent and subtracting the product from H (Alexander, 1982). We divided I_B by R to determine the total energy release or heat per unit area (HA) of the fire (Rothermel and

Deeming, 1980). Reaction intensity (I_R), the rate of energy release per square meter of flaming zone, was calculated by dividing I_B by flame depth (FD) (Albini, 1976; Alexander, 1982).

We timed the combustion duration of ten fecal pats from the moment of ignition until they were fully consumed by combustion. This was accomplished by following the main head fire as closely as safety would allow and tagging the burning pats with colored flags when they came into view through the smoke. Duration of combustion (DC) was considered to include the inclusive time after passage of the flame front until heat could no longer be detected by tactile sense.

To determine the combustion characteristics of fecal pats, we ground the oven-dried fecal pats to a fine powder using a Wiley grinder mill followed by a Udy grinder mill. Ground samples were stored in separate numbered containers and oven-dried for several additional days. We pressed the oven-dried fecal material into 1-g pellets and combusted them in a bomb calorimeter to determine high heat of combustion (HH). We calculated the adjusted high heat of combustion (HH_{adj}) for vaporization of water by subtracting 1,263 kJ/kg from HH. Low heat of combustion of the fecal pats (FH_{adj}) was calculated as per fine fuels. Next, we multiplied FH_{adj} by the weight of the consumed fuel (FW) to derive the heat released per unit area (FHA) in kJ/m^2, which had no variation as a result of using a mean value of FW for each patch. Finally, we calculated the rate of energy consumption of fecal pats (FI_R) in kJ/m^2/sec by dividing FHA by DC and converting to kW/m^2. We compared the mean combustion characteristics of fecal pats to the behavior of the grass fires using

Pearson's correlation at the 0.05 significance level. SAS version 6.04 was used for the correlation analyses (SAS, 1985).

RESULTS AND DISCUSSION

The September grassland fire had a lower intensity than either the December or April fire (Table 2). The lower intensity was a result of the live vegetation at the time of burning. The growing season for this tallgrass region extends into early October and the vegetation in September had not yet begun to senesce and cure, so the higher fuel moisture reduced fire spread.

Correlations between fecal pat combustion characteristics and fine-fuel fire behavior were generally high, but not significant, with p-values > 0.05 in every case (Table 3). Fecal pat combustion characteristics and fine fuel fire behavior were negatively associated except for comparisons involving the duration of combustion of fecal pats.

Despite the lower intensity of the grassland fire in September, the fecal pats consumed in the September burn exhibited the highest rate of energy consumption and burned with the greatest heat per unit area (FHA) among the three burns (Table 2). Fecal pat consumption rates were similar for December and April, but the FHA of fecal pats burned in April was almost twice that of fecal pats burned in December. Energy content of fecal pats was similar for all three burn patches, with September, December, and April fecal pats exhibiting similar high heats of combustion (range of 14,070 to 14,870 kJ/kg).

Fecal pat combustion characteristics varied as a result of the different environmental conditions associated with each grassland fire. The April burn was conducted under the lowest RH, lowest fine fuel moisture, and highest wind speed, which is reflected in the higher intensity of the April grassland fire. Despite the higher intensity of the April fire, combustion of the fecal pats was slower in April than September. The April grassland fire was not ignited until late afternoon, so the lack of intense solar radiation at the time of burning, may have been a factor in the lower combustion rate for fecal pats in April. Conditions for the September fire included a relatively high RH and fine-fuel moisture level, but the KBDI the day before the September burn was within the range of high drought conditions, reflecting drier dead fuels as compared to fuels in the April or December fires (Table 1). The September burn was also conducted at mid-day, so solar radiation was more intense and direct during the September fire than in the April fire. The December burn was conducted with a higher RH and lower ambient temperature than either September or April, which possibly accounts for lower energy consumption rates for fecal pats during that burn even though the fine-fuel load and KBDI were relatively high.

Differences in total mass among fecal pats also influenced combustion characteristics. The fecal pats burned in September had almost twice the total mass of fecal pats collected in December or April, even though all fecal pats had a similar density and area of contact with the soil among the three burn patches (Table 1). The greater mass of fecal pats burned in September resulted in greater FI_R and FHA.

The heat released per unit area of fecal pats was extreme for all three grassland fires. Heavy concentrations of woody fuels burned under high drought conditions release less energy (22,700 kJ/m^2) (Andrews and Rothermel, 1982). When environmental conditions result in a KBDI level above 300, as was associated with each of the three fires, the soil beneath burning fuels may experience some loss of organic material as a result of combustion (Melton, 1989). Because of differences in FHA associated with the fecal pats consumed in each of the three grassland fires, the potential disturbance intensity of burning fecal pats in terms of heat directed at the soil was greatest for fecal pats consumed in the September fire and least for fecal pats consumed in the December fire.

CONCLUSIONS

Bison fecal pats may have been the most abundant and wide-spread form of small-scale disturbance on pre-European settlement tallgrass prairie. Small scale ($< 2\text{-m}^2$) disturbances may increase species diversity within a plant community by allowing certain non-matrix plant species to compete for resources (Gibson, 1989). A high density of local small-scale disturbances may have a cumulative regional influence (Parish and Turkington, 1990; Glenn *et al.*, 1992). An unburned fecal pat is a form of small-scale disturbance that can influence its local area in several ways (Marsh and Campling, 1970; MacDiarmid and Watkin, 1971). Although the ecological implications of burned fecal pats on plant regrowth following a grassland fire have never been studied to our knowledge, the extreme levels of heat energy that can be released from burning bison fecal pats under certain conditions may represent an important source of spatial heterogeneity in plant communities.

Because fires conducted under drought conditions can burn with sufficient intensity to remove organic material from the soil, the prolonged exposure to extreme high heat on the soil directly beneath burning fecal pats may significantly influence plant regrowth by killing underlying seeds and rhizomes, leaving a small gap open to succession. Areas of heat-sterilized soil left beneath burned bison fecal pats may be important factors contributing to biodiversity and patchiness within some plant communities.

The negative associations between fecal pat combustion characteristics and fine fuel fire behavior indicate that bison fecal pats and fine-fuels belong to different fuel-moisture lag classes. The tallgrasses represent one-hour time lag fuels which respond quickly to changes in environmental conditions (Nelson, 1969; Wright and Bailey, 1982). Fecal pats are more dense and compact than fine-fuels, behaving more like fuels in longer time-lag classes. The fecal pats may retain sufficient moisture to slow energy consumption rates or prevent ignition even though fine-fuels are extremely dry. Likewise, the fecal pats may absorb moisture more slowly after long periods of dryness and may burn readily when fine-fuels are moist and fire intensity is low. Similar differences in fire behavior between fuels of varying lag times have been documented (Nelson, 1969).

Varying moisture and density of duff can alter fire temperature and its effect on the soil (Frandsen and Ryan, 1986). Similarly, the moisture level, density, and mass of a fecal pat at the time of burning may determine its influence on surrounding plant regrowth. The greater mass of the fecal pats burned during the September fire resulted in a greater amount of heat directed to the soil than fecal pats burned in April or December. The greater mass may indicate that the majority of the fecal pats on the September burn patch may have been deposited when forage moisture and insect activity were low resulting in highly viscous fecal material that remained in intact clumps rather than flowing into smooth, flat pats or disintegrating. Because mass can influence the combustion characteristics of fecal pats, the time year at which the fecal pats are produced may represent yet another source of potential variability within plant communities resulting from the presence of burned bison fecal pats.

We have shown that burning bison fecal pats release high levels of heat energy directed to small areas. As such, they can represent an intense small-scale disturbance on tallgrass prairie. Varying environmental conditions can influence the level of intensity associated with the disturbance. It is possible that a prairie with a high density of fecal pats of varying age and moisture levels can, once burned, exhibit greater species diversity than a similar prairie with no fecal pats. Considering the vast herds of bison that once occupied the prairie, the fecal pats they produced may be an important factor to consider in prairie restoration projects and deserves further study.

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TABLE 1.—Weather, fuel conditions, and fecal pat characteristics associated with tallgrass fires conducted in September 1995, December 1995, and April 1996. KBDI values were determined from the MESONET climatological station at Foraker, Oklahoma.

	September 1995	December 1995	April 1996
Relative humidity (%)	50	62	16
Air temperature (°C)	30	14	26
Wind speed (km/hr)	7	14	20
Solar radiance (mJ/m2)	733	219	445
K/B Drought Index	601	493	428
Fine Fuel load (kg/ha)	6,640	9,480	6,560
Fine fuel moisture (%)	72	16	6
Fecal pat:			
moisture (%)	8	37	9
mass per fecal pat (g)	130	60	67
density (g/cm^3)	0.22	0.23	0.21
area (cm^2)	250	270	230

TABLE 2.—Fire behavior and fecal pat combustion characteristics associated with three tallgrass prairie fires. Values are means (± SE) calculated from three measurements.

Parameter	September 1995	December 1995	April 1996
Grass fire			
Fireline intensity (kW/m)	920 ± 110	11,990 ± 1,590	17,040 ± 910
Reaction intensity (kW/m^2)	1,620 ± 590	3,950 ± 140	2,640 ± 540
Heat per unit area (kJ/m^2)	9,605 ± 1,040	15,190 ± 2,115	10,350 ± 540
Fecal pats			
Energy consumption (kW/m^2)	42 ± 5.7	5 ± 0.5	4 ± 0.2
Heat per unit area (kJ/m^2)	74,340	29,210	44,030
Duration of combustion (min.)	36 ± 6	112 ± 13	194 ± 9

TABLE 3.—Pearson correlation coefficients expressing the degree of association between fecal pat combustion characteristics and fire behavior parameters of three tallgrass prairie fires. No significant associations were found at the $P < 0.05$ level.

Fecal pat combustion characteristics	Grassland fire behavior		
	I_B (kW/m)	I_R (kW/m^2)	HA (kJ/m^2)
FI_R (kW/m^2)	-0.96	-0.82	-0.52
FHA (kJ/m^2)	-0.87	-0.93	-0.31
DC (min.)	0.97	0.42	0.88

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