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Landscape-level interactions between topoedaphic features and nitrogen limitation in tallgrass prairie

Tracy L. Benning[1] and Timothy R. Seastedt
Department of Environmental, Organismic and Population Biology and Institute of Arctic and Alpine Research, University of Colorado, Boulder, CO 80309, USA

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Abstract

Transects across watersheds with varying fire histories and remotely-sensed data were used to study vegetation-resource interactions in a tallgrass prairie in Kansas. Paired plots (fertilized, control) were established along these transects and sampled for grass and forb biomass during the 1989 and 1990 growing seasons. Fertilization resulted in significant production responses in grass and total biomass on the west slopes of the annually burned (1D) and infrequently burned (N4) watersheds for both years ($p = 0.05$). In 1989, fertilization also produced a significant increase in grass biomass on the west slope of the unburned transect ($p = 0.05$), however, total production was not significantly increased. East slopes were insensitive to nitrogen additions. Differences in production response along these transects were assessed by testing the interaction between fertilization response and slope position. Significant interactions occurred on both 1D and N4, but only in 1990.

Production data for both years were also compared to Normalized Difference Vegetation Index (NDVI) values derived from thematic mapper (TM) images for 1989 and 1990. When differences among transects or watersheds were statistically different, a positive relationship between NDVI and biomass was observed. NDVI values accurately reflected the spatial patterns of production along these transects for both years although not necessarily the magnitude.

Introduction

Understanding how vegetation-resource interactions vary across landscapes has become the focal point of much ecological research. Many studies have identified nutrient availability to be an important factor controlling net primary productivity (NPP) (Aber *et al.* 1978; Pastor and Post 1986; Vitousek and Howarth 1991; Schimel *et al.* 1991; Seastedt *et al.* 1991). Characterizing spatial variability in resources and subsequent productivity at the landscape level is critical for accurately predicting rates of ecosystem processes (Schimel *et al.* 1991). In this study, we examined the spatial variability in nitrogen limitation and how this factor was influenced by fire frequency and topoedaphic controls in a tallgrass prairie.

Plant productivity in tallgrass prairie is strongly influenced by fire and climate (Hulbert 1969; Old 1969; Towne and Owensby 1984; Abrams *et al.* 1986). Fire alters the energy environment of prairie vegetation (Knapp 1984, 1985) and affects nutrient

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[1] Current address: Department of Biological Sciences, Stanford University, Stanford, CA 94305

cycling (Raison 1979; Kucera 1981; Risser and Parton 1982; Ojima *et* al. 1990). Aboveground biomass production in mesic, ungrazed grasslands generally increases following a fire during years with normal precipitation (Towne and Owensby 1984). This increased production has been attributed to release of readily available nitrogen and phosphorus from plant material, increased nitrogen mineralization rates, enhanced nitrogen fixation and altered microclimatic conditions, including improved light availability (Daubenmire 1968; Old 1969; Raison 1979; Biederbeck *et* al. 1980; Knapp and Seastedt 1986; Hulbert 1988). Most of these effects occur immediately after the fire.

Annual fires, in tallgras prairie may have several long-term effects such as decreasing soil organic matter and changing species composition (Old 1969; Kucera 1981; Risser *et* al. 1981; Ojima *et* al. 1990). These long-term effects result in the loss of labile soil organic matter and large losses of nitrogen through volatilization and immobilization (Daubenmire 1968; Biederbeck *et* al. 1980). Consequently, nitrogen limitation is a general characteristic of fire-maintained tallgrass prairie ecosystems. Understanding how landscape-related patterns in soil properties might affect this nitrogen limitation is a key factor in predicting patterns of NPP in tallgrass prairie.

Most of the preliminary information concerning nitrogen limitation comes from information derived from small plot experiments and CENTURY model simulations. Ojima (1987) modified the CENTURY model (Parton *et al.* 1987) to study the effects of fire on prairie productivity and nitrogen dynamics. The model predicted greater productivity on infrequently burned sites or long-term unburned sites in the year in which they were burned due to greater nitrogen availability in these areas. The model also predicted that nitrogen availability to plants would be influenced by the previous year's productivity. This was based on changes in the soil immobilization potential incurred by root detritus production and accumulation (Chapin *et al.* 1986). The amount of carbon-rich detritus produced by the previous years growth should be large on annually burned sites (Seastedt 1988; Seastedt and Ramundo 1990; Benning and Seastedt, submitted). In contrast, reduced root production on unburned sites should reduce the soil nitrogen immobilization potential of these areas. Therefore, the model predicted that N limitation should be greatest on annually burned sites. Spatial variability in nitrogen under a single fire regime is not explicitly addressed by the model, and this study will examine this issue. Net primary productivity will also vary across a water availability gradient (*e.g.* Sala *et* al. 1988; Knapp *et al.* 1993); hence, such patterns should induce nitrogen immobilization gradients directly related to net primary productivity. These gradients are locally created by variation in topography and soil depth and should be important when addressing landscape-level phenomenon.

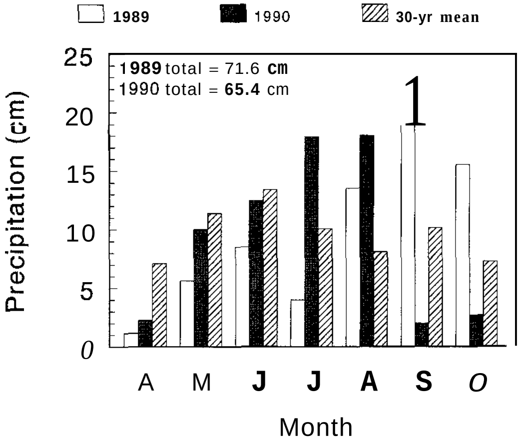

Fig. 1. Growing season precipitation and the 30-year mean for 1989 and 1990. (A = April through O = October).

Table 1. Transect characteristics for each watershed.

	UB	1D	N4
Orientation	E–W	E–W	E–W
Average soil depth	20 cm	36 cm	29 cm
Range of soil depth	6–50 cm	7–50 cm	5–50 cm
Length	240 m	410 m	340 m
# of slope positions	12	24	20
Fire history	unburned	annually burned	burned every 4 years (last burned in 1988)

Topoedaphic features are particularly important

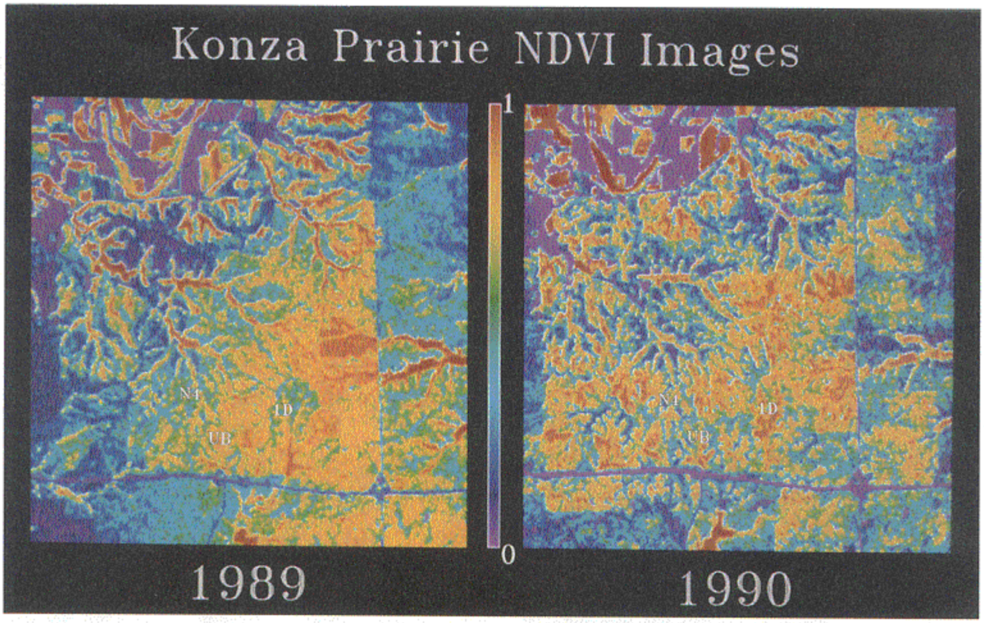

Fig. 2. Normalized Difference Vegetation Index (NDVI) images for August 4, 1989 and September 7, 1990. These images have been radiometrically normalized using pseudoinvariant features. Konza Prairie Research Natural Area is bordered by interstate I-70 to the south and highway 177 to the east. Watershed units used in this study are indicated on the image. Higher NDVI values correspond to higher greenness.

at Konza Prairie Research Natural Area, in the Flint Hills of NE Kansas, due to their complex nature. Topographic position is believed to be significant because of the juxtaposition of layers of impermeable shale and fractured limestone resulting in a 'stair-step' appearance which at any given point may contain a number of different soil types and depths (Jantz *et al.* 1975). Certain areas on some watersheds also appear to be supplemented with water and dissolved nitrogen from regions originating both within and between watersheds. Lateral movement of water and dissolved nutrients are facilitated by the impermeable shale. As a consequence of these topoedaphic features, certain areas within any given watershed should be more sensitive to nitrogen limitation than others. While nitrogen, light and water are the important controlling factors of net primary productivity in the tallgrass prairie, light limitation is usually uniform across any given fire regime (Knapp *et al.* 1993). Thus, it should be the interaction of nitrogen and water availability that ultimately controls patterns of productivity observed across such landscapes. The null hypothesis being tested is that nitrogen fertilization along these topographic gradients will result in a uniform productivity response.

This study was designed to complement the landscape-level studies of Schimel *et al.* (1991) and Knapp *et al.* (1993). Schimel *et al.* (1991) demonstrated that variation in net primary productivity across watersheds was correlated with light interception and leaf nitrogen. Water availability was also recognized as varying inversely with topographic position, but no measurements were made. In Knapp *et al.* (1993) the question of spatial variability in water as an important controlling factor of net primary productivitty was addressed. In both watersheds studied, net primary productivity was strongly correlated with volumetric soil water content. The objectives of the present study were: 1) to document the spatial variability in nitrogen limitation and net primary productivity due to topoedaphic controls and 2) to determine if this variabil-

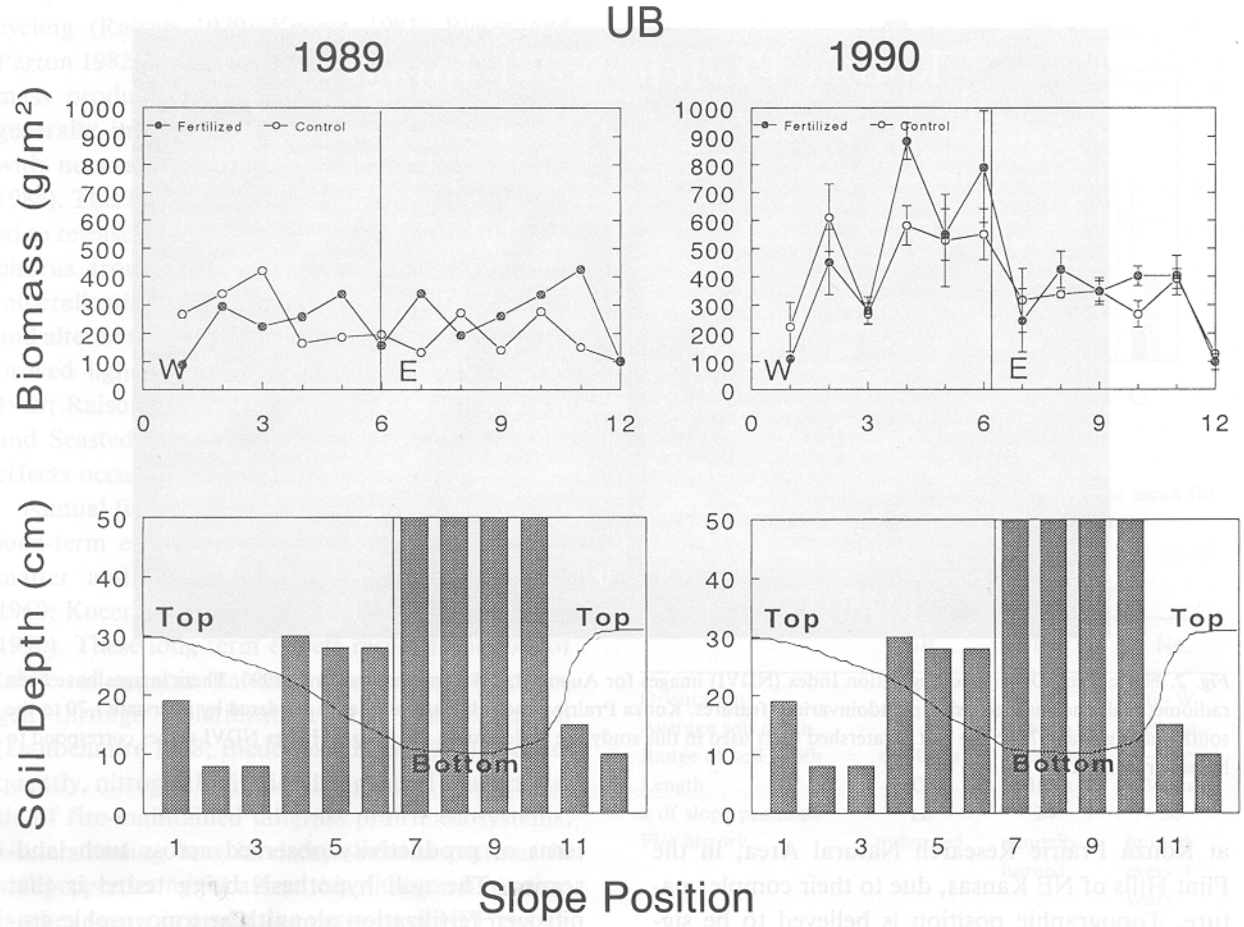

Fig. 3. Total net primary productivity as a function of slope and soil depth for the unburned watershed (UB). The transect extended from west to east with the west slope transect (W) consisting of slope positions 1–6 and the east slope transect (E) consisting of slope positions 7–12. The transect profile and soil depths are shown in the bottom figures. Transect profile refers to the relative topographic arrangement of the slope positions across the transect. In 1990, each value is the mean of four plots for both fertilized and control.

ity is expressed in vegetation indices calculated from remotely-sensed data.

Study site and methods

This study was conducted at Konza Prairie Research Natural Area, located 10 km south of Manhattan, Kansas (39°3′ N latitude, 96°3′ W longitude). Vegetation in this area is dominated by warm season C_4 grasses such as big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Andropogon scoparius* Michx.) and Indiangrass (*Sorghastrum nutans* (L) Nash.) (Hulbert 1988). Rainfall for the area averages 83 cm yr^{-1}; mean January temperature is –2.7°C and mean July temperature is 26.6°C (Brown and Bark 1971; Bark 1987). Precipitation patterns for study years relative to the 30-year average reported by Bark (1987) are typical of the large interannual variability characteristic of this region (Fig. 1).

Net primary production

An annually burned watershed (1D), an unburned watershed (UB) and a watershed with a four year

Table 2. Effects of fertilization and fertilization * slope position on aboveground net primary productivity in 1989 and 1990 for the unburned watershed (UB).

UB: Variable	df	1989 F-value	p	1990 F-value	p
Grass:					
Fertilized **W**	1	5.47	0.0475	0.92	0.3423
Fert*Slope **W**	1	4.23	0.0738	1.67	0.2024
Fertilized E	1	0.90	0.3505	0.00	0.9484
Fert*Slope E	1	0.40	0.5297	0.01	0.9102
Forb:					
Fertilized **W**	1	0.62	0.4549	0.76	0.3890
Fert*Slope **W**	1	0.39	0.5490	1.52	0.2236
Fertilized E	1	0.84	0.3672	0.00	0.9648
Fert*Slope E	1	0.22	0.6423	0.01	0.9367
Total:					
Fertilized **W**	1	2.37	0.1619	1.65	0.2055
Fert*Slope **W**	1	1.94	0.2008	3.15	0.0828
Fertilized E	1	2.41	0.1312	0.00	0.9672
Fert*Slope E	1	0.88	0.3544	0.02	0.8914

W-west slope, E-east slope.

fire frequency (N4) (last burned in 1988) were chosen to establish transects. Transects were installed across these watersheds in an east-west direction. Transects began and ended on uplands with the exception of the transect on N4, it began in the lowland and ended in an upland. Transect characteristics are shown in Table 1. Paired, 1 x 1 m plots (fertilized, control) were established at approximately 20 m intervals along each transect. Each set was assigned a corresponding numerical slope position. In 1990, these paired plots were replicated for a total of four fertilized and four control plots at every slope position. For both years, fertilizer plots received an additional 20 g/m^2 of nitrogen in the form of ammonium nitrate. Aboveground net primary productivity estimates were made by harvesting all aboveground live plant material from $0.1-m^2$ quadrats in each plot during August, the time of peak total community biomass (Abrams *et al.* 1986). Harvested plant material was separated into live grass and live forb components, dried and weighed. Litter production was estimated similarly from the dead plant mass, however, this production data was collected by Konza Prairie LTER. Soil depth was estimated at each plot using a T-handled soil probe, pushed into the soil until contact with bedrock. This was performed ten times for each plot and averaged to obtain soil depth at each slope position. Maximum measurable depth was 50 cm, which is an underestimate of soil depth in the lowlands. Weather data for the study period were provided by the Konza Prairie LTER program. Analysis of covariance was used to determine if significant fertilizer and interaction (fertilizer * slope position) differences occurred in grass, forb and total biomass measurements. Fertilizer effects were evaluated using a standard ANOVA procedure. Means for litter production were compared using a standard two sample t test.

Remote sensing measurements

Landsat-5 thematic mapper (TM) images were obtained for August 4, 1989 and September 7, 1990. Both images were radiometrically normalized using pseudoinvariant features according to the technique developed by Schott *et al.* (1988). A normalized difference vegetation index (NDVI) image was created for each date (Fig. **2).** The difference in acquisition dates for the images should be minimized by using a greenness index. In tallgrass prairie, plant phenology varies little from year to year and biomass generally peaks in early August (Abrams *et al.* 1986). An additional month in the 1990 growing season should not significantly increase NDVI relative to an August image (Turner *et al.* 1992).

Images were then rectified using **USGS** topographic quadrangle maps with a scale of 1:24,000 (7.5 min) for locating ground control points. **A** cubic convolution resampling was used to correct the geometric distortion of the images (Lillesand and Kiefer 1987). Transects across watersheds were sampled from the vegetation index images corresponding to the approximate location of the transects on the ground. Each transect was a single pixel wide by the same approximate length as the ground transect. A single image pixel for thematic mapper data is **30** x **30** m (excluding band 6), therefore the

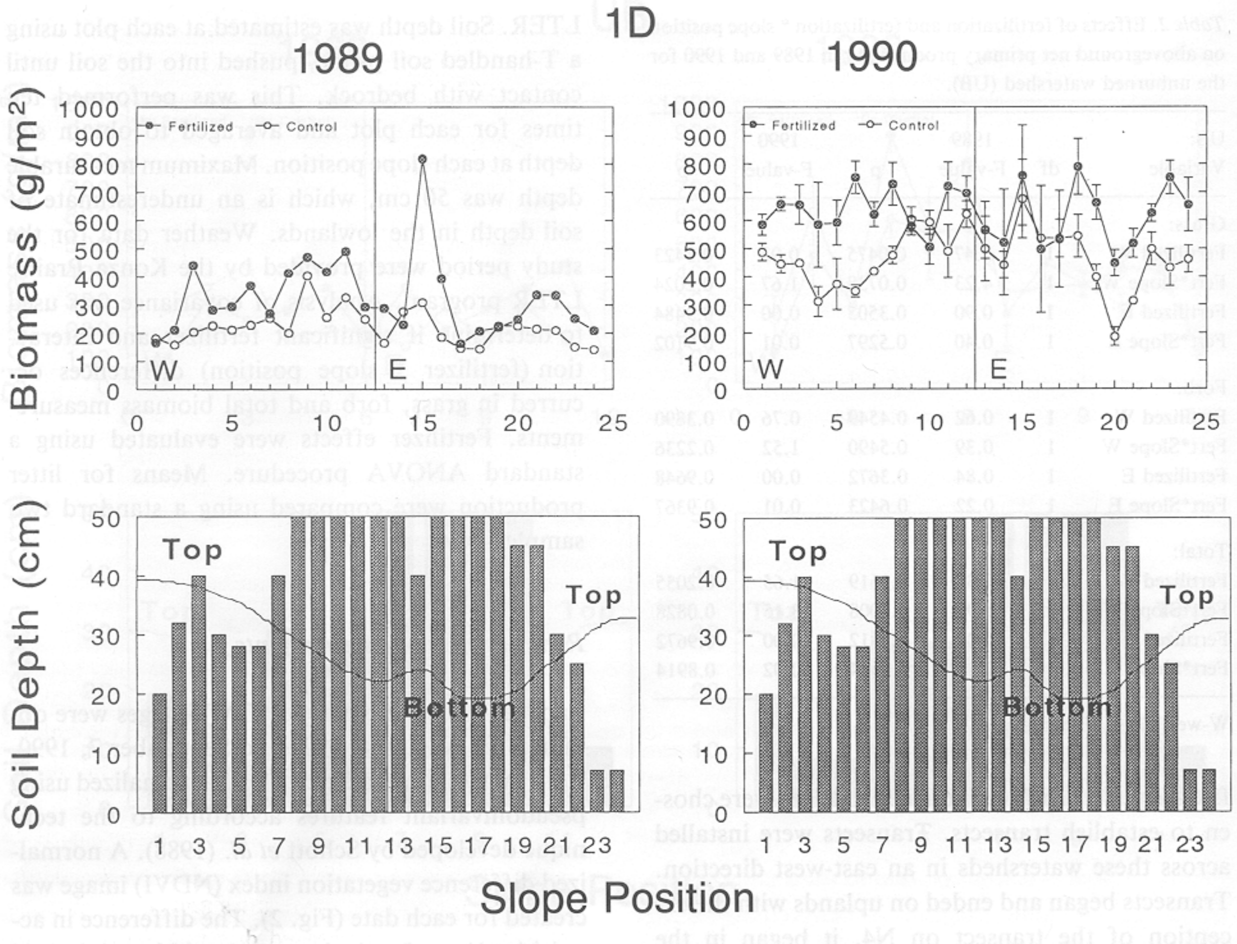

Fig. 4. Total net primary productivity as a function of slope and soil depth for the burned watershed (1D). The transect extended from west to east with the west slope transect (W) consisting of slope positions 1–12 and the east slope transect (E) consisting of slope positions 13–24. The transect profile and soil depths are shown in the bottom figures. Transect profile refers to the relative topographic arrangement of the slope positions across the transect. In 1990, each value is the mean of four plots for both fertilized and control.

transect on 1D would be 1 pixel by 14 pixels or 30 × 420 m. Each image transect was replicated once. The extracted pixel values were then averaged for each slope position.

Results

Landscape patterns in aboveground productivity and response to fertilization were variable depending on watershed and year. Differences in growing season precipitation patterns likely accounted for some of the variation. Precipitation patterns differed between the years even though growing season totals were similar (Fig. 1). Soil moisture was below normal entering 1989 due to a previous drought year (Knapp *et al.* 1993). Large precipitation events at the end of the 1989 growing season (August and September) ended the drought (Fig. 1). Precipitation patterns in 1990 were more similar to the 30-yr mean (Knapp *et al.* 1993).

Landscape patterns in productivity and response to fertilization in the unburned watershed (UB) are shown in figure 3. In 1989, the uplands and the

Table 3. Effects of fertilization and fertilization * slope position on aboveground net primary productivity in 1989 and 1990 for watershed 1D.

1D: Variable	df	1989 F-value	p	1990 F-value	p
Grass:					
Fertilized **W**	1	7.11	0.0107	26.36	0.0001
Fert*Slope **W**	1	0.12	0.7292	8.83	0.0038
Fertilized E	1	0.95	0.3331	2.58	0.1113
Fert*Slope E	1	0.00	0.9723	5.03	0.0273
Forb:					
Fertilized **W**	1	0.43	0.5174	2.55	0.1138
Fert*Slope **W**	1	1.65	0.2058	10.02	0.0021
Fertilized **E**	1	1.46	0.2313	3.74	0.0561
Fert*Slope E	1	0.99	0.3226	2.67	0.1058
Total:					
Fertilized **W**	1	6.08	0.0177	19.61	0.0001
Fert*Slope **W**	1	0.41	0.5242	2.75	0.1008
Fertilized E	1	2.31	0.1335	0.97	0.3283
Fert*Slope E	1	0.33	0.5690	2.72	0.1023

W-west slope, E-east slope.

lowland supported similar amounts of NPP, consequently, no landscape patterns in net primary productivity were evident. Fertilization resulted in a significant grass production response on the west slope transect in 1989 (Table 2). In 1990, productivity in the western upland was greater than in the lowland or eastern upland (Fig. **3).** This was somewhat unexpected because the soils at these slope positions were only slightly deeper than the rest of the uplands in this transect. As in 1989, there was no overall production response due to fertilization in 1990, but at slope positions 4 and 10, there was a localized production response (Table 2 and Fig. 3).

The annually burned watershed (1D) contained less variation in soil depth and a much deeper average soil depth than UB (Table 1). Highest net primary production was measured in the lowland and the lowest values were found in the uplands for both years (Fig. 4). In 1989, fertilization of 1D resulted in a significant productivity response in both grass and total biomass for the west slope transect, however, there was no significant interaction between slope position and fertilization (Table 3); an indication that the increase in production was uniform across the topographic gradient (Fig. 4). In 1990, the greatest increase in production due to fertilization occurred in both uplands (Fig. 4). Fertilizer additions in the lowlands produced only two locally significant production responses at slope positions 11 and 18 (Fig. 4). Fertilization produced a significant increase in grass and total biomass on the west slope transect and forb biomass on the east slope transect (Table 3). There was a significant interaction between fertilization and slope position for grass and forb biomass on the west slope transect and grass biomass on the east slope transect (Table 3). Therefore, the response due to fertilization was not to the same magnitude at every slope (Table **3).**

Watershed N4, the infrequently burned watershed, had the most topographic variation and an intermediate average soil depth (Table 1). Consequently, this watershed exhibited strong landscape-level controls on patterns of net primary productivity (Fig. 5). Greatest net primary production occurred in the lowland and the lowest occurred in the upland for both years. However, the production range was greatly reduced in 1989, a low precipitation growing season. Both grass and total biomass productivity were increased due to fertilization in both years (Table 4). The response was only marginally significant in 1989, but highly significant in 1990 (Table 4). In contrast to 1D, most of the significant production increases occurred in the lowland (Fig. 5). In 1990, both grass and total biomass productivity produced significant interaction terms (Table 4). Again, indicating that there was a differential production response at individual slope positions.

Transect slope position measurements of total net primary production were averaged to obtain watershed level estimates of productivity (Fig. **6).** In 1989, production in the control plots was similar across all three watersheds. Fertilization increased production the greatest amount on 1D, followed by N4. Productivity did not increase on UB due to fertilization. In 1990, total biomass in the control plots was greatest on 1D with total biomass productivity similar on UB and N4. Fertilization produced the

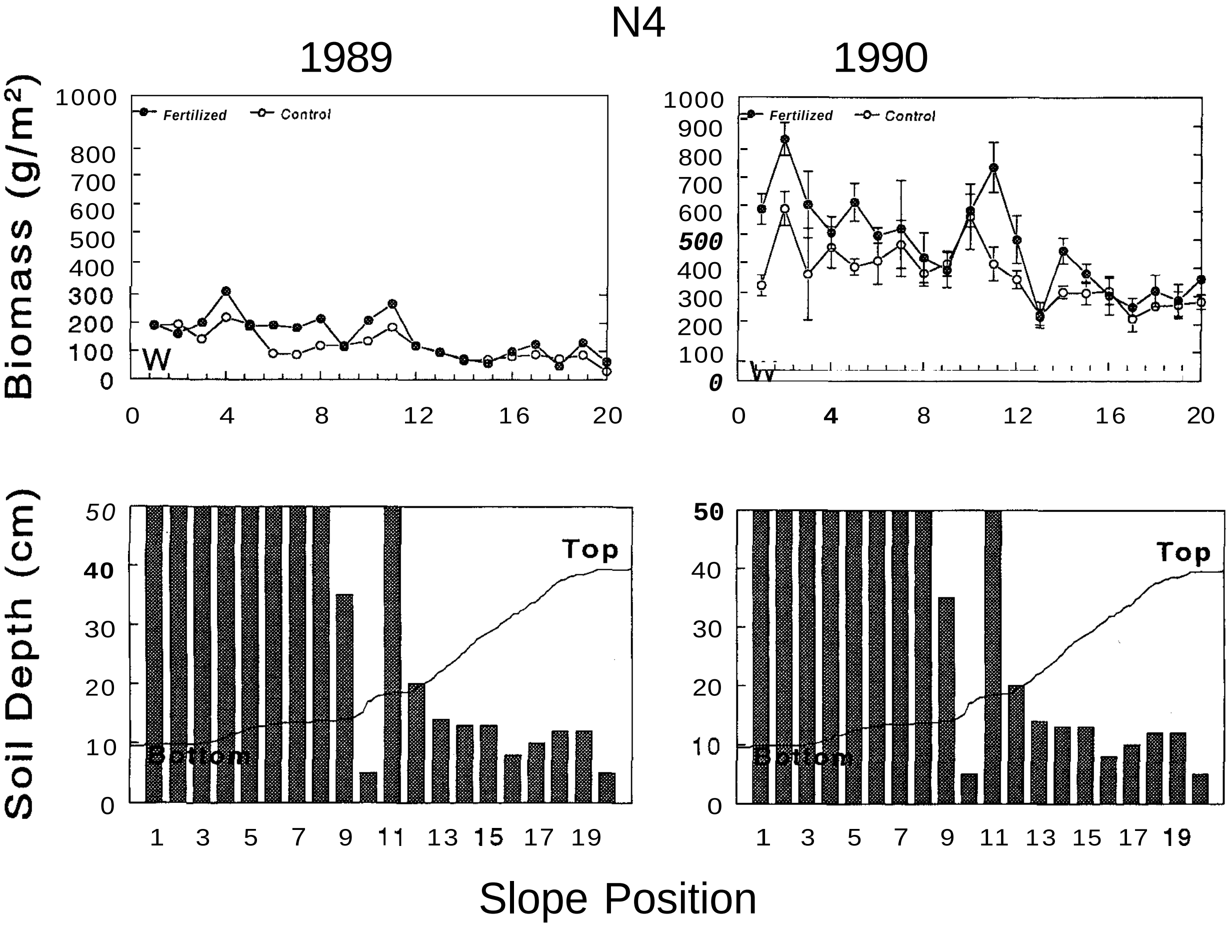

Fig. 5. Total net primary productivity as a function of slope and soil depth for the infrequently burned watershed (N4). The transect extended from west to east with the west slope transect (W) consisting of slope positions 1–20. The transect profile and soil depths are shown in the bottom figures. Transect profile refers to the relative topographic arrangement of the slope positions across the transect. In **1990,** each value is the mean of four plots for both fertilized and control.

largest production responses on 1D and N4 with no increase in production due to fertilization on UB.

Normalized Difference Vegetation Index (NDVI) patterns across the transects were remarkably similar to the patterns for biomass on all transects (Fig. 7). NDVI patterns reflected the reversal in biomass trends observed between 1989 and 1990 growing seasons for both UB and 1D. NDVI values were highest on the west slopes of both transects, again consistent with biomass measurements. The NDVI patterns on N4 were much more similar between the two years then would be expected from biomass measurements (Fig. 7). Values at each slope position were generally not significantly different from one year to the next even though there was a substantial increase in total biomass and litter in 1990 (Fig. 6, Fig. 7 and Table 5). Litter production data also showed a significant increase on UB in 1990 (Table 5). When NDVI values were averaged across transects to obtain a watershed-level estimate of NDVI and compared to transect averaged estimates of total biomass (Fig. 6), the correlations were neigher strong nor significant. However, NDVI values were also extracted for the entire watershed and compared to biomass estimates obtained for the

Table 4. Effects of fertilization and fertilization * slope position on aboveground net primary productivity in 1989 and 1990 for watershed N4.

N4: Variable	df	1989 F-value	1989 p	1990 F-value	1990 p
Grass:					
Fertilized	1	3.90	0.0519	14.10	0.0002
Fert*Slope	1	2.53	0.1159	4.92	0.0280
Forb:					
Fertilized	1	0.54	0.4627	0.77	0.3824
Fert*Slope	1	0.93	0.3389	0.02	0.9001
Total:					
Fertilized	1	3.74	0.0568	16.04	0.0001
Fert*Slope	1	1.35	0.2498	4.80	0.0299

Only west slope was included in study.

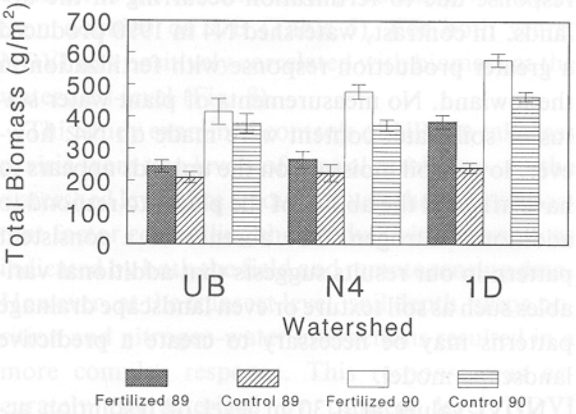

Fig. 6. Average total net primary productivity along each transect by watershed. Each value is the mean of the individual slope position totals.

watersheds from LTER data. In this case, the correlations were much stronger and significant for both years (Fig. 8).

Discussion

Burning creates a relatively constant light and thermal regime for early spring plant production. However, the ability of plants to exploit these conditions is regulated by water and available nutrients. At Konza Prairie Research Natural Area, the unique interaction of parent material, fire frequency and slope results in complex spatial patterns of net primary productivity. In tallgrass prairie, it is commonly presumed that landscape patterns of net primary productivity are defined by gradients in water availability (Abrams *et al.* 1986). Our results suggest that within the landscape, either nitrogen, water or both may limit productivity at any particular topographic position. Self-shading limitations may also be experienced in the most productive sites. However, at the watershed level, fire frequency and the subsequent nitrogen limitation is the

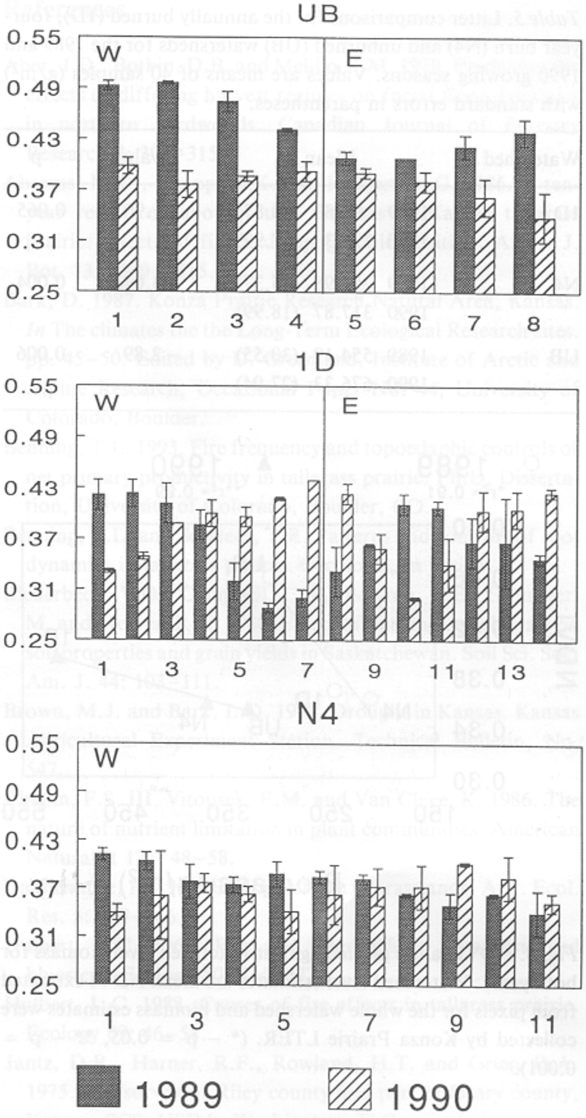

Fig. 7. NDVI values by slope position for each transect. Each value is the mean of two pixels taken adjacent to one another at each slope position.

Table 5. Litter comparisons for the annually burned (1D), four-year burn (N4) and unburned (UB) watersheds for the 1989 and 1990 growing seasons. Values are means of 40 samples (g/m^2) with standard errors in parentheses.

Watershed	Mean			T-value	P
1D	1989	99.80	(8.87)	−1.90	0.065
	1990	127.3	(7.99)		
N4	1989	257.98	(15.37)	−3.043	0.004
	1990	317.87	(18.99)		
UB	1989	554.19	(30.55)	−2.89	0.006
	1990	676.33	(27.94)		

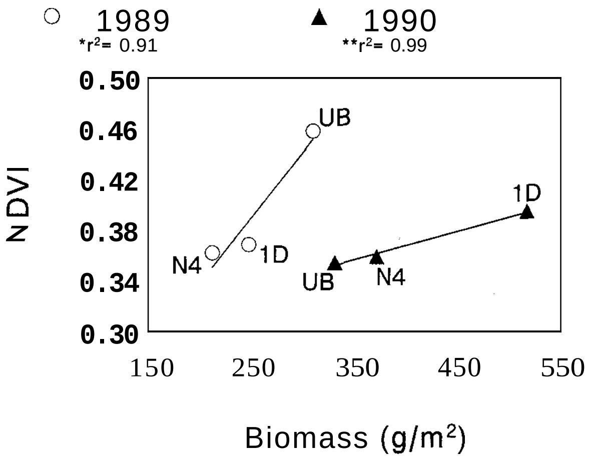

Fig. 8. **NDVI** values plotted against watershed level biomass for both years. Watershed level estimates are mean NDVI extracted from pixels for the whole watershed and biomass estimates were collected by Konza Prairie LTER. (* – p = 0.05, ** – p = 0.001).

overwhelming factor controlling the production response (Knapp and Seastedt 1986; Seastedt *et* al. 1991). For example, fertilization produced a significant productivity response on annual or infrequently burned watersheds, but not on the unburned watershed for both years (Fig. 6). The 1989 growing season was characterized by visible signs of drought stress such as low canopy height and leaf rolling in grasses (Knapp *et al.* 1993). Net primary productivity was severely reduced, and there were no significant differences in productivity for the three watersheds (Fig. 6). Even under these conditions, however, additional nitrogen resulted in a 16% increase in total biomass on N4 and a 38% increase on 1D. At this level of spatial resolution, which, historically was addressed with only small plot studies, nitrogen availability appears to be an important limiting factor and directly related to fire frequency (Seastedt *et al.* 1991).

Knapp *et* al. (1993) reported that 1990 volumetric soil water content and total soil moisture measured on UB and 1D did not differ significantly between watersheds over the entire growing season, however, within watersheds both parameters exhibited significant landscape patterns. Data on plant water stress showed that minimum water stress occurred in the lowlands where nitrogen availability appeared to be the highest (Schimel *et al.* 1991; Knapp *et* al. 1993). Our results from the annually burned watershed in 1990 show the greatest production response due to fertilization occurring in the uplands. In contrast, watershed N4 in 1990 produced a greater production response with fertilization in the lowland. No measurements of plant water status or soil water content were made on N4; however, lower soil moisture on the uplands appears to have affected the ability of the plants to respond to additional nitrogen. The absence **of** a consistent pattern in our results suggests that additional variables such as soil texture or even landscape drainage patterns may be necessary to create a predictive landscape model.

NDVI values at a 30 m level of resolution accurately characterized trends in biomass production. Overall, productivity patterns on the watersheds during the two years were very different, as reflected in both total biomass and NDVI values at both the transect and watershed level (Fig. 6, 7 and 8). In 1989, a drought year, fire was more detrimental to productivity where water was a limiting factor (*i.e.* the lowlands of 1D and N4). This pattern is evident in the transect-level NDVI values for that year (Fig. 7). NDVI values extracted at the watershed level showed greater contrast (Fig. 8). Average NDVI was much higher on UB than on 1D or N4. However, there were no significant differences in average production among watersheds for these control plots (Fig. 6). This does not appear to be consistent with differences in biomass among these watersheds. Schimel *et al.* (1991) reported that canopy nitrogen mass was generally positively correlated with biomass. In addition, during the 1989 growing season, nitrogen uptake was lower in the unburned watershed overall, however, nitrogen concentration per unit mass or per unit leaf area was generally higher for UB. This would account for the higher NDVI values measured for UB without a corresponding increase in biomass in 1989. Higher nitrogen concentrations in the foliage resulted in a substantially 'greener' canopy signal.

Productivity in the 1990 growing season was as predicted based on fire frequency (Fig. *6)*. The annually burned watershed 1D had the most production and also the highest NDVI values. There were no differences in productivity between N4 and UB, both unburned in 1990, and the NDVI values for these watersheds were also similar (Fig. *6* and 8). In contrast to the fact that litter production was more than doubled on UB (Table 5). For both years, NDVI was positively correlated with biomass at the watershed-level (Fig. 8).

This study examined controls of NPP in tallgrass prairie from two levels of spatial resolution. At the watershed level, fire frequency was the most important factor controlling the productivity response as indicated by both the field and remote sensing data. However, at the transect level, soil depth, slope position and nitrogen-water interactions resulted in a more complex response. This response was accurately characterized by transect level NDVI values but was poorly correlated to biomass when both were 'scaled-up' to predict watershed level responses. Because of the complex nature of the transect NPP response, multiple transects at different locations within the watersheds may provide better estimates for scaling-up purposes.

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