IN-43-CR
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Final Technical Report

p.212

Submitted to

National Aeronautics and Space Administration

FIFE Guest Investigator Program

Goddard Space Flight Center

NAG-5-897

The influence of grazing on surface climatological variables of tallgrass prairie.

(FIFE SRB-6)

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(NASA-CR-190315) THE INFLUENCE OF GRAZING ON SURFACE CLIMATOLOGICAL VARIABLES OF TALLGRASS PRAIRIE Final Technical Report (Kansas State Univ.) 212 p

N92-24897

CSCL 02C

Unclas

G3/43 0089403

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Introduction

Mass and energy exchange between most grassland canopies and the atmosphere are mediated by grazing activities. Ambient temperatures can be increased (Timson 1989) or decreased (Seastedt and Briggs 1989) by grazers. Data we have assembled from simulated grazing experiments on Konza Prairie Research Natural Area and observations on adjacent pastures grazed by cattle show significant changes (increases and decreases) in primary production, nutrient content, and bidirectional reflectance characteristics as a function of grazing intensity (Dyer et al. 1991, Turner et al. in press). The purpose of our research was to provide algorithms that would allow incorporation of grazing effects into models of energy budgets using remote sensing procedures. Our approach involved 1) linking empirical measurements of plant biomass and grazing intensities to remotely sensed canopy reflectance and 2) using a high resolution, mechanistic grazing model (Coughenour 1984) to derive plant ecophysiological parameters that influence reflectance and other surface climatological variables.

Experimental Studies

METHODS

In 1987, two field experiments were conducted to examine the role of grazing on ecosystem-level parameters which affect measurements obtained during FIFE. Both experiments were conducted on Konza Prairie Research Natural Area, one in a monoculture of Bromus inermis, an introduced, cool season grass, and the second in native tallgrass prairie. Both sites were located independently from established FIFE Intensive Sites. Experimental manipulations included four simulated grazing regimes ranging from no grazing to severe grazing, implemented by uniformly mowing small plots to 5-, 10-, or 20-cm heights or leaving unmowed or by mowing to ground level 0, 1, 3, or 6 times during the growing season. These mowing manipulations allowed us to evaluate foliage removal in terms of the relative quantity of leaf area removed per unit area per time period (grazing intensity) and how often foliage removal events occurred (grazing frequency). Biomass production, standing crop of vegetation, N content of foliage and N production estimates were obtained periodically through the growing season using standard techniques. Spectral reflectance measurements also were obtained throughout the growing season and in conjunction with vegetation sampling. For more detailed descriptions of methodology see Dyer et al. (1991), Turner (1990), Turner et al. (in press).

In addition, observational studies were conducted at 12 FIFE Intensive Sites in 1987 and 1988. Six of these sites (FIFE sites 6912-PAM, 8639-SAM, 0847-SDC, 4268-BRK, 1246-BRL and 1445-BRL) were grazed by cattle, with grazing intensities ranging from light to heavy. Of the remaining sites, three (FIFE sites 2731-DCP, 3129-BRK, and 3414-BRK)

were ungrazed sites from which senescent vegetation from the previous growing season had been removed by burning in early May and three (FIFE sites 2132-BRK, 2139-PAM and a site adjacent to 2731-DCP) were ungrazed sites left unburned. Observations from FIFE Intensive Sites provided data to compare with experimental plots and to establish the generality of our results. Biomass production, standing crop of vegetation, N content of foliage and N production estimates were obtained using moveable and permanent exclosures in 1987 and 1988. Spectral reflectance measurements were obtained throughout the 1987 growing season. For more detailed descriptions of methodology see Turner (1990), Turner et al. (in press).

RESULTS

Bromus inermis experimental plots

Aboveground biomass production was significantly related to mowing height. Season-long production for 5-cm (664.4 g/m^2) and 10-cm (629.0 g/m^2) plots were 22 and 29% greater than that for unmowed controls (514.8 g/m); the 20-cm plots showed the same level of productivity as controls. Nitrogen content of aboveground tissues and cumulative nitrogen production (incorporation of N into aboveground tissue) was significantly higher on all mowing treatments compared to controls. Standing crop biomass was reduced significantly by mowing (5-cm height was reduced 67-70% compared to controls).

Normalized Difference Vegetation Index (NDVI) and greenness index (results of Principal Components Analysis) derived from reflectance data were poorly correlated with biomass. Correlation of NDVI with N content of foliage was stronger, particularly if

stratified by mowing height. In plots simulating heavy grazing where aboveground vegetation was sparse and soil become more exposed from above the canopy, the utility of NDVI as an predictor of vegetation status decreased significantly.

For more detailed discussion of results see Dyer et al. (1991).

Tallgrass prairie experimental plots and grazed pastures

Vegetation responses. Mowing frequency significantly affected season-long grass biomass and nitrogen production. Mean biomass production on plots mowed 1, 3, and 6 times was 19%, 38%, and 61% greater, respectively, than on unmowed plots. Nitrogen production on plots mowed 1, 3, and 6 times was 1.7, 3.3, and 4.3 times greater, respectively, than on unmowed plots. Mowing resulted in elevated foliar concentrations of nitrogen and phosphorus throughout the growing season compared to concentrations on unmowed plots.

Aboveground grass biomass and N production was significantly affected by mowing height. Plots mowed to 5-, 10-, and 20-cm heights produced 32%, 42%, and 54% more biomass, respectively, than unmowed plots by late August. At the end of the growing season, 5-, 10-, and 20-cm plots had produced 13%, 21% and 26% more biomass, respectively, than unmowed plots. Mowing resulted in increased N concentrations and production in direct relation to the intensity of mowing. N concentrations were significantly higher on mowed plots than on unmowed plots at every sampling date after day 141. By late August, N production was 2.2-2.5 times higher on mowed plots than on unmowed plots.

On grazed pastures, grazing intensity varied widely within season and between years (1987 and 1988). Standing crop of grasses was inversely related to grazing intensity in both years. In 1987, grasses at all sites except one appeared to compensate for foliage removal by

grazing indirect proportion to amount of foliage removed. Compensation resulted in season-long biomass production similar to that on ungrazed plots despite large differences in the proportion of production removed by cattle. Seasonal trends in N concentrations were positively correlated with grazing intensity in both years.

Remote sensing measurements. On mowing frequency plots, mowing altered the seasonal pattern of the NDVI observed on unmowed control plots. On mowed plots, NDVI values were much lower immediately after mowing than on unmowed controls and increased between mowings to values close to or greater than unmowed values. By late in the growing season, NDVI values on plots mowed one or three times attained levels higher than that on unmowed plots, while NDVI values on plots mowed six times were lower.

On mowing height plots, NDVI was significantly affected by mowing height and day of year, with day of year accounting for 25% and height accounting for 44% of the variability. Height treatment differences in NDVI corresponded to differences in standing crop brought about by mowing. NDVI was highest throughout the season on unmowed plots where standing crop was greatest and lowest on plots mowed to 5 cm, where standing crop was least. Differences between treatments were greatest early in the season, when the mean NDVI for 5-, 10-, and 20-cm plots was approximately 60%, 85%, and 95% of that on unmowed plots, respectively. By midseason, treatment differences in NDVI were smaller but generally consistent with differences in aboveground biomass. Within treatment fluctuations in NDVI also corresponded to changes in biomass. NDVI increased between mowings and these increases were greatest early in the season when plant growth rates were greatest.

Reflectance in all wavelength bands was a function of mowing height. For most of

the season, reflectance of visible wavelengths was higher and reflectance of near infrared (NIR) wavelengths was lower on mowed plots than on unmowed controls. Mean reflectance of visible wavelengths on mowed treatments was as much as 60% greater in early summer, approximately the same in late summer and up to 31% greater in fall relative to unmowed plots. Mean reflectance of NIR wavelengths on mowed treatments was as much as 31% less in early summer, 15% less in late summer and approximately the same in fall compared to unmowed plots.

Reflectance characteristics observed on the mowed plots were generally consistent with those observed when grazers were responsible for manipulations of biomass and N content. NDVI on grazed pastures was significantly affected by management practice (grazed, burned, and unburned) and day of year. Until midseason, mean NDVI on unburned sites averaged 90% of that on burned and mean NDVI on grazed sites averaged 85% of that on burned sites. After midseason, mean NDVI on grazed sites was approximately equal to that on burned sites whereas mean NDVI on unburned sites was approximately 90% of that on burned sites. Variability in NDVI was greatest on grazed sites during the first half of the growing season. During the second half of the growing season grazed site variability was approximately equal to that on unburned sites, but it was still greater than that on burned sites.

Reflectance versus canopy characteristics. The relationship between NDVI and canopy characteristics (%N, N mass, and biomass) on experimental plots varied with season. Early in the growing season (day 167), NDVI was strongly related to %N, N mass, and biomass. Late in the growing season (day 243), NDVI was not significantly related to any

canopy characteristic. At the end of the growing season (day 301), when plant material was largely dead, NDVI was significantly related to %N and biomass but not to N mass. In general, NDVI was more strongly related to canopy characteristics early in the season (R^2 = 0.62-0.76) than later in the season (R^2 = 0.06-0.43).

The relationship between NDVI and canopy characteristics on sites grazed by cattle also varied over the growing season. There were strong linear relationships between NDVI and all plant characteristics during June-July, but not over longer periods. NDVI was significantly related to N mass during June-October.

For more detailed discussion of results see Turner (1990), Turner et al. (in press).

DISCUSSION

Our results show dramatically that Bromus inermis and the dominant tallgrass prairie grass species, as is the case with many C_3 and C_4 grasses, respond to repeated grazing (on experimental plots mowing was used as a surrogate of grazing) by altering productivity when compared to ungrazed controls. The type of change is a function of the degree of removal and has been described empirically and theoretically by several workers in terms of the Herbivore Optimization Curve (McNaughton 1979, Hilbert et al. 1981, Dyer et al. 1982, 1986, Williamson et al. 1989, and others) as well as in the theoretical models of the dynamics of plant quality in response to herbivory (Edelstein-Keshet 1986). The response is known for may different species in grasslands throughout the world. In many cases processes associated with grazing regulate a large amount of the variance in productivity during any one growing season.

The responses to experimental manipulations we observed are relatively straightforward. Even though standing crop was highest on unmowed control plots, throughout the growing season mowed plots produced more than controls. These responses are biologically significant in several ways. They point to the importance of understanding grassland productivity under stress, but also focus attention on the inherent difficulty of determining grassland function by relying on instantaneous measures of biomass, particularly if taken in ungrazed portions of grazed sites, or in grazed pastures if response to grazing is not accounted for.

Analysis of covariance of individual radiometer band values, with standing crop as the covariate (Dyer et al. 1991), showed that reflectance from the plant canopy is independent of dry biomass per se. This result reaffirms older reports that structural components alone are not the main basis for determining the amount of absorption or reflectance, but other properties contained within the plant, mainly water and chlorophyll (Tucker 1979), are the largely responsible. Thus, if biomass (or its equivalent, leaf area) is not the main source of variation, and since N (the main contributor to chlorophyll development) varies according to mowing treatment or grazing intensity, if follows that a primary contributor of remotely sensed radiation is the internal state of the plant. In our experiments and observations we take this to be both the qualitative and quantitative N status within the plant. This is an important factor in measuring canopies that are influenced by grazing. Total instantaneous biomass is reduced temporarily, but at the same time the plant's metabolic status can be increased significantly, one of the net results being that total N is increased. Therefore, changes in leaf area or total biomass that affect absorption or reflectance as a function of

grazing may be offset by concomitant changes due to nitrogen or water status.

The treatment and site differences in NDVI that we observed were closely related to defoliation induced changes in plant canopies. Large increases in biomass (and NDVI) occurred over relatively short periods following defoliation. Changes in N concentrations and allocation patterns following defoliation by grazers reduced the usefulness of NDVI as an indicator of biomass and leaf area. NDVI-biomass relationships were season-specific, with sensitivity of this relationship minimized at midseason.

Simulation Modeling

A study of grazing effects on FIFE measurements was initiated using a mechanistic simulation model. Funding provided in years 2 and 3 of this project was not sufficient to allow us to complete the analyses. The model, designated GRASS, was assembled from information in North America and first applied to problems in the Serengetti grasslands of Africa (Coughenour 1984). The model is composed of a series of submodels that provide interactions among abiotic and biotic elements in grasslands including: 1) atmospheric components, 2) radiation and energy balance, 3) soil water, 4) photosynthesis (plant specific by metabolic type and age class), 5) plant water, 6) above- and belowground plant growth by age class, and 7) nitrogen uptake and distribution. Included in the input-output array are 1) transpiration and evaporation, 2) radiation interception, and 3) leaf area indices. Over 100 biotic and abiotic parameters are required to run the model. Most are available from literature values, and from FIFE and NSF-LTER data on Konza Prairie. Initial parameterization of the model has been completed but further refinement will be required.

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NAG-5-897 Supported Publications:

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Sumitted to Journal of Geophysical Research

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Effects of Management and Topography on the Radiometric Response of a Tallgrass Prairie

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Bidirectional reflectance measurements were obtained on grazed, burned ungrazed, and unburned ungrazed tallgrass prairie in eastern Kansas. Observations were also made on experimental plots on which vegetation height and biomass were manipulated by mowing. Foliage biomass and productivity (including off-take estimates) were measured concurrently at all sites. While productivity of mowed or grazed sites was either equal to or greater than that on unmowed or ungrazed sites, individual or cumulative Normalized Difference Vegetation Index (NDVI) values tended to be positively correlated with biomass, not productivity. NDVI on grazed prairie was lower than on burned and unburned prairie during the first half of the growing season. After midseason, NDVI on grazed prairie was higher than on unburned prairie but no different than on burned prairie. Strong linear relationships between NDVI and canopy nitrogen and biomass existed early and late in the growing season, but not at midseason. These relationships suggest that plant physiological processes associated with regrowth following defoliation are dominant influences on reflectance early in the season, whereas the accumulation of senescent material is the dominant process affecting reflectance in the latter half of the growing season. Canopy temperature was related to canopy nitrogen and biomass at midseason. The use of NDVI to estimate plant productivity and vegetation-atmosphere exchange is complicated by changes in plant characteristics induced by grazing or mowing. Grazing tends to homogenize potential landscape-induced differences in vegetation activity. Factors otherwise useful in estimating plant production, such as burning treatment and soil depth, are not strongly correlated with above-ground biomass or NDVI under grazing conditions. Results presented here suggest that concurrent use of thermal information provided by some satellite sensors may improve this relationship.

INTRODUCTION

The Normalized Difference Vegetation Index (NDVI) has been variously termed an index of plant vigor, an indicator of the photosynthetic capacity of a vegetated surface, and the amount of illuminated chlorophyll present [Sellers et al., 1988]. Fundamentally, the index is a ratio assembled from red and near-infrared (NIR) spectral values. Canopy changes (for example, leaf area, biomass, and nitrogen content) often inversely alter the absorption of radiation in the red and near-infrared spectrum, thereby making NDVI particularly sensitive to canopy changes [Tucker, 1979]. Both absorbed photosynthetic radiation and grassland biomass have been accurately predicted using satellite NDVI values [Kanemasu et al., 1989].

Models of biological processes and radiative transfer in plant canopies have recently been combined to provide a synthesis of the relationships between vegetation indices obtained from remote sensing instruments and plant physiological processes [Sellers, 1985, 1987]. The accuracy of these models depends strongly on the relationships between variables affecting plant activities and canopy characteristics. Rigorous evaluation of the importance of these factors requires experimental manipulations [Dyer et al., 1991]. A major factor affecting the physiological status of grassland vegetation is grazing, which potentially influences canopy reflectance characteristics as strongly as do different surface cover types. Changes in canopy characteristics following grazing include (1) reduction in above-ground biomass, (2) increased nitrogen (N) concentration in remaining tissue, and (3) reduced or retarded accumulation of senescent plant material through the growing season. Collectively, these changes suggest that grazed vegetation should have a larger NDVI per unit of biomass or leaf area than ungrazed vegetation. However, grazing may also expose the soil surface, and by introducing another surface with its own spectral properties, substantially influence reflectance.

In this study we attempted to determine whether defoliation alters the reflectance characteristics of tallgrass prairie in predictable ways compared to undefoliated tallgrass canopies and to determine the relationships between grazing-induced changes in plant canopies and NDVI. A series of hill slope transect measurements were used to relate these findings to landscape level assessments of NDVI conducted by Davis et al. [this issue]. Reflectance measurements were obtained on experimental plots on which vegetation height, biomass, and leaf area were manipulated by mowing. This allowed us to evaluate grazing effects in terms of the relative quantity of leaf area consumed per unit area per time period (grazing intensity) and how often these grazing events occurred (grazing frequency). Observations from long-term grazed pastures provided data to compare with experimental plots and to establish the generality of our results.

METHODS

Study Area

Research was conducted in 1987 on the Konza Prairie Research Natural Area (KPRNA), located in the Flint Hills of northeastern Kansas approximately 12 km south of Manhattan, Kansas, and on six other sites within 12 km of KPRNA selected for study during the First International Satellite Land Surface Climatological Project (ISLSCP) Field Experiment (FIFE) [Sellers et al., this issue]. The dominant vegetation of this area consists of warm-season tallgrass prairie species, including big bluestem (Andropogon gerardii Vitman), Indian grass (Sorghastrum nutans (L.) Nash) and switch grass (Panicum virgatum L.) [Freeman and Hulbert, 1985].

Reflectance Measurements

Bidirectional spectral reflectance measurements were obtained with an Exotech Model 100-A radiometer. The Exotech radiometer measured reflected radiation in two discrete wavelength bands in the visible (B1 = 0.50-0.60 and B2 = 0.60-0.70 μm) and two in the NIR (B3 = 0.70-0.80 and B4 = 0.80-1.10 μm) regions of the spectrum. The radiometer had a 15° field of view and was attached to a portable frame in nadir position approximately 1.5 m above the soil surface. The area sampled by the radiometer was approximately 0.1 m^2. Measurement periods were limited to a period within 2 hours of solar noon on clear days. Measurements were referenced to a $BaSO_4$ calibration panel and reflectance was calculated from a ratio of canopy radiance to that of the reference panel. Reflectance measurements were used to calculate NDVI using the formula, NDVI = [B4 - B2] / [B4 + B2].

Reflectance measurements were obtained on experimental plots on which tallgrass prairie was mowed to simulate foliage removal by cattle. In the grazing intensity experiment, the canopy was maintained at a height of 5 cm, 10 cm, or 20 cm above the soil surface or was left unmowed. In the grazing frequency experiment, vegetation was mowed to about 2 cm above the soil surface 0, 1, 3, or 6 times during the 1987 growing season [Turner, 1990]. Reflectance measurements were obtained at intervals of 4-16 days on grazing intensity plots and 3-32 days on grazing frequency plots. On each observation date, three-five reflectance measurements were obtained and a mean was calculated for each plot. Treatment means for each date were calculated from six replicates of the four treatments in the intensity experiment and five replicates of the four treatments in the frequency experiment. An estimate of surface temperatures on intensity experiment plots was obtained on day 196 (July

15) using the thermal channel of a Barnes Model 12-1000 modular multiband radiometer.

Spectral reflectance measurements were also obtained on 12 sites representative of three management practices common to the Flint Hills region. Six of the sites were grazed by cattle: FIFE sites 19(6912-PAM), 21(8639-SAM), 29(0847-SDC), 32(4268-BRK), 40(1246-BRL), and 42(1445-BRL). Of the remaining sites, three were ungrazed sites from which senescent vegetation from the previous year had been removed by burning in early May: sites 1(2731-DCP), 8(3129-BRK), 10(3414-BRK). The other three sites were ungrazed sites left unburned: sites 6(2132-BRK), 31(2139-PAM), and a site adjacent to site 1. Tallgrass prairie is commonly burned to maximize plant production for grazing and hay production. All grazed sites had been burned prior to the initiation of new growth in the spring. Hereafter, these sites will be referred to as the grazed, burned, and unburned treatments, respectively. At least 25 canopy reflectance measurements were taken on transects at each site at intervals of 1-26 days through the growing season. On sites located on hill slopes, two transects were used, one oriented parallel and the other perpendicular to the contour. Observations were spaced at intervals of approximately 2 m along transects. Mean reflectances were calculated for each treatment for 1 to 12-day intervals in 1987 centered on the following dates: day 154 (June 3), day 177 (June 26), day 184 (July 3), day 222 (August 10), day 229 (August 17), day 232 (August 20), day 258 (September 15) and day 280 (October 7).

Vegetation Sampling

Vegetation on intensity experiment plots was sampled immediately following measurement of reflectance on day 167 (June 16), day 243 (August 31), and day 301 (October 28), during FIFE intensive field campaigns (IFCs) 1, 3, and 4, respectively [Sellers et al., this issue].

Estimates of total (live plus dead) above-ground biomass, nitrogen concentration in above-ground grass tissue (indicated as %N), and N mass (grams of nitrogen per square meter) in grass foliage were obtained for each plot. Estimates of these canopy characteristics on each grazed site were obtained during the intervals for which mean reflectances were calculated [Turner, 1990].

In contrast to the experimental plot measurements, which were made on a single soil type and topographic position, hill slope transects were established to evaluate the effect of factors correlated with topographic position (for example, soil depth and soil moisture) on plant biomass on various combinations of burned or unburned, grazed or ungrazed pastures. Results from ungrazed sites are reported by Schimel et al. [1991]. Here we summarize how grazing influences landscape-level measurements of plant biomass and N mass using data collected on transects established near FIFE site 42.

Analysis

Effects of mowing intensity or management practice and season on NDVI were analyzed using a split plot design where the whole plot factor was mowing height or management practice and the split plot factor was day of year. The error term for whole plot factors was plot or site within treatment variance. This design accommodated repeated measurements of the same sites or plots over time. NDVI values ranged between 0 and 1 and were transformed using an arcsine-square root transformation [Zar, 1984] prior to analysis. A similar procedure was used on %N data and for an analysis of differences in the coefficients of variation observed for specific treatments. NDVI was linearly regressed to %N, N mass, and biomass obtained from intensity experiment plots on days 167, 243, and 301 and from grazed sites.

RESULTS

Frequency of Foliage Removal

Mowing altered the seasonal pattern of the NDVI observed on unmowed control plots (Figures 1a-1d). The pattern on unmowed control plots was characterized by relatively high NDVI values in June, which gradually decreased as senescent material accumulated over the growing season. On mowed plots, NDVI values were much lower immediately after mowing than on unmowed controls and increased between mowings to values close to or greater than unmowed values (Figure 1). By late growing season, NDVI values on plots mowed one or three times attained levels higher that on unmowed plots, while NDVI values on plots mowed six times were lower.

Intensity of Foliage Removal

Analysis of variance (ANOVA) results indicated that NDVI was significantly affected by mowing height and day of year (Table 1) and there was a significant interaction between mowing height and day of year. Over 90% of the variability in NDVI values was accounted for by the model; day of year alone explained 25% of the variability and height alone explained 44%. Height treatment differences in the NDVI corresponded to differences in biomass brought about by mowing. NDVI was highest throughout the season on unmowed plots where biomass was greatest and lowest on plots mowed to 5 cm where biomass was least (Figure 2a). Differences between treatments were greatest early in the season when the mean NDVI for 5-cm, 10-cm, and 20-cm plots was approximately 60%, 85%, and 95%, of that on control plots, respectively. By midseason, differences between treatments were smaller but generally consistent with differences in above-ground biomass.

Growing season fluctuations in NDVI within height treatments also corresponded to changes in biomass. Low NDVI values on days 155, 175, and 190 were obtained 1-2 days after mowing (Figure 2a), whereas high NDVI values on days 167 and 187 were obtained 12-13 days after mowing. Increases in NDVI between mowings were greatest early in the season when plant growth rates were greatest. By midseason, plant growth rates were lower, less biomass accumulated between mowings, and less frequent mowing was required to maintain the plots at treatment heights.

Within-date variability in NDVI on experimental plots was small, with coefficients of variation (CV) ranging between 1.5% and 8% over the season (Figure 2b). CV was significantly affected by mowing height and day of year, and there was a significant interaction between mowing height and day of year (Table 1). Sampling variability in NDVI tended to be highest on plots mowed to 5 cm and lowest on plots mowed to 20 cm and unmowed plots.

Reflectance in all wavelength bands was a function of mowing height (Figure 3). For most of the season reflectance of visible wavelengths was higher (Figures 3a and 3b) and reflectance of NIR wavelengths was lower (Figures 3c and 3d) on mowed plots than on unmowed controls. For visible wavelengths, much less difference between treatments and control plots was observed when differences in biomass were least, for example, on days 187, 223, and 243 when biomass had accumulated for 12, 33, and 20 days, respectively, following mowing. Mean reflectance of visible wavelengths on mowed treatments was as much as 60% greater in early summer (June 4 - July 15), approximately the same in late summer (August 3

- July 15) and up to 31% greater in fall (September 21 - October 7) relative to unmowed plots. Mean reflectance of NIR wavelengths on mowed treatments was as much as 31% less in early summer, 15% less in late summer and approximately the same in fall compared to unmowed plots.

Grazing and Burning

Findings from the mowed plots were generally consistent with those observed when grazers were responsible for manipulations of biomass and N content. ANOVA results indicated that NDVI was significantly affected by management practice (grazed, burned and unburned; $P < 0.05$) and day of year ($P < 0.0001$), with no significant interaction between these factors. Approximately 91% of the variability in NDVI values was accounted for by the model; day of year accounted for 68% and management accounted for 9% of the variability. Mean NDVI values for all management practices declined over the growing season (Figure 4). Until midseason, mean NDVI on unburned sites averaged 90% of that on burned and mean NDVI on grazed sites averaged 85% of that on burned sites. After midseason, mean NDVI on grazed sites was approximately equal to that on burned sites whereas mean NDVI on unburned sites was approximately 90% of that on burned sites.

Coefficients of variation in NDVI ranged from 3.5 to 8.5% for burned sites, 8.0 to 12.5% for grazed sites, and 6.9 to 9.2% for unburned sites over the growing season and were significantly affected by management practice ($P < 0.02$) and day of year ($P < 0.01$) with no significant interaction between factors. These factors accounted for approximately 79% of the variability in coefficients of variation of NDVI. Variability was greatest on grazed sites during the first half of the growing season. During the second half of the growing season grazed site variability was approximately equal to that on unburned sites, but it was still greater than that on burned sites.

Mean reflectance in each wavelength band for burned and grazed treatments is presented in Figure 5. Reflectance in B2 was consistently greater on grazed areas until midseason (Figure 5b). Reflectance of NIR wavelengths was consistently lower on grazed areas than on burned areas until late in the season (Figures 5c and 5d). Mean reflectance of visible wavelengths on unburned areas was higher than that on burned areas (by 7-26%) throughout the growing season. Reflectance of NIR wavelengths on unburned areas was about 11% lower in early summer, about 6% lower in late summer, and no different from burned areas in fall.

Reflectance versus Canopy Characteristics

The relationship between NDVI and canopy characteristics (%N, N mass, and biomass) varied with season (Figure 6 and Table 2). Early in the growing season (day 167), NDVI was strongly related to %N, N mass, and biomass. Late in the growing season (day 243), NDVI was not significantly related to any canopy characteristic. At the end of the growing season (day 301), when plant material was largely dead, NDVI was again significantly related to %N and biomass but not to N mass. In general, NDVI was more strongly related to plant characteristics early in the season (R^2 = 0.62-0.76) than later in the season (R^2 = 0.06-0.43).

The relationships between NDVI and plant characteristics on sites grazed by cattle also varied over the growing season. Too few observations were available for analyses to be conducted by season. Data were therefore grouped into the following periods for analysis: June-October, June-September, and June-July (Table 3). There were strong linear relationships between NDVI and all plant characteristics for June-July data. These decreased in strength as the analysis period was extended. NDVI was significantly related to only N mass for June-September and June-October data.

Grazing and Topography

The FIFE site consists of uplands frequently dissected by drainage networks [cf. Davis et al., this issue]. Schimel et al. [1991] demonstrated correspondence between this topographic variation and canopy characteristics on four ungrazed watersheds in the site. They found a significant correlation between soil depth (reflecting hill slope position and bedrock geology) and live above-ground grass biomass ($P < 0.06$; see Table 4 and Figure 7a). Both soil moisture and nutrient availability were suggested as causal agents for this relationship. There was also a significant correlation between live N mass and soil depth (Table 4 and Figure 7a).

On grazed watersheds, these relationships were disrupted ($P > 0.5$; see Table 4 and Figure 7b). Landscape control of biomass accumulation was modified by patchy removal of plant material by grazers. The spatial distribution of biomass and N mass established in grazed watersheds by late May 1987 (IFC 1) persisted throughout the growing season (Figure 8). The persistence of the initial grazing-influenced pattern of biomass on the landscape is likely maintained by repeated grazing of the same areas [Hobbs et al., 1991].

DISCUSSION

NDVI and Management

Seasonal trends in NDVI on unmowed experimental plots (Figures 1a and 2a) and burned and unburned sites (Figure 4) were similar to those previously reported for tallgrass prairie at KPRNA [Sellers et al., 1988] and in experiments reported by Dyer et al. [1991]. One major difference, however, was that our observations were initiated too late to record the "green-up" period observed in previous studies. In 1987, the canopy had reached "peak greenness" by the end of May.

The seasonal profile of NDVI was affected by grazing and burning management. Burning increased NDVI throughout the season, reflecting removal of senescent material early in the season and enhanced biomass production on these sites [Seastedt et al., 1991]. Defoliation resulted in decreases in NDVI values during most of the growing season on both experimental plots and grazed sites. Moreover, reflectance in all wavelength bands was affected by defoliation, with reflectance of visible wavelengths increased and reflectance of NIR decreased on defoliated canopies.

The effect of foliage removal on seasonal trends in NDVI was dependent on the frequency and timing of mowing. NDVI values were low following mowing and increased as biomass accumulated, an observation also reported by Dyer et al. [1991]. Recovery of NDVI to levels comparable to those on unmowed plots was rapid under the favorable plant growth conditions existing during 1987. Similar responses at a shorter time scale were observed on intensity experiment plots. The magnitude of the response was greater early in the growing season when grass growth rates were high and on plots clipped closest to the soil surface than late in the season and on plots on which greater biomass remained after mowing (Figure 2a). Repetition of this pattern during the growing season depends largely on regrowth potential of the vegetation.

Treatment and site differences in NDVI were closely related to defoliation-induced changes in canopies measured at these sites. These changes, discussed below, included (1) reduction in above-ground biomass, (2) increased N concentration in remaining tissue, (3) exposure of the soil surface, and (4) reduced accumulation of senescent plant material through the growing season. These changes were highly correlated: on experimental plots, variation in N concentration, soil surface exposure, and senescent material accumulation was accomplished by varying above-ground biomass using several intensities of defoliation. On grazed sites, above-ground biomass was manipulated by consumption by cattle.

Biomass. Although NDVI and related NIR/red ratio vegetation indices have been widely used for estimation of biomass, the utility of such relationships depends upon a number of factors [Dyer et al., 1991]. When significant relationships between NDVI and biomass existed in data from our intensity plots and grazed sites, they were season specific. Weiser et al. [1986] reported relationships between spectral reflectance measures and biomass in tallgrass prairie that were both site- and year-specific. Richardson et al. [1983] reported that a single linear relationship fit the data for NIR reflectance and above-ground biomass collected in June and September, although the coefficient of determination was higher for data in June than in September (0.82 versus 0.70). Kleman and Fagerlund [1987] reported that the NIR/red ratio was strongly related to the biomass of barley, until significant amounts of senescent material had accumulated. In addition, the relationships between the ratio and biomass were different at each observation date.

Although the range of biomass on grazing intensity plots was large at all sampling dates, the range in NDVI values was considerably larger early in the season than at other sample dates. Growth rates also were greatest early in the growing season; little biomass accumulated after August 31 (day 243) except on unmowed plots [Turner, 1990]. This suggests that plant physiological processes associated with regrowth following defoliation, such as development of new structural tissues and N uptake and concentration, are dominant influences on reflectance early in the season, whereas the accumulation of senescent material is the dominant process affecting reflectance in the latter half of the growing season.

Disproportionately high allocation of N to the upper canopy may also account for the lack of relationship between biomass and NDVI at midseason [Dyer et al., 1991]. As biomass increases and light limitation occurs in the lower canopy, N allocation to the upper canopy increases [Hirose et al., 1988; Schimel et al., 1991]. Under these conditions NDVI may be less dependent on total foliage biomass than on nitrogen rich chlorophyll concentrations in the upper canopy, or on interactions between the two [Dyer et al., 1991].

Nitrogen. Significant negative relationships between canopy reflectance of visible wavelengths and %N have been reported for grasses [Richardson et al., 1983; Everitt et al., 1985] and loblolly pine [Nelson et al., 1986]. In winter wheat, canopy N content is positively related to NIR/Red ratios [Hinzman et al., 1986]. These studies related %N to reflectance over naturally occurring N gradients or manipulated %N (via fertilization) regimes, and no effort was made to separate the effects of %N and biomass on reflectance. Increased leaf area and biomass, reduced exposure of the soil surface, and higher chlorophyll concentrations resulting from increased N availability have been cited to account for N-related canopy reflectance characteristics [Walburg et al., 1982; Hinzman et al., 1986; Kleman and Fagerlund, 1987]. Here, the two measures of N (%N and N mass) were inversely related. The concentration of nitrogen in above-ground grass tissue, which increased with defoliation intensity, was higher throughout the season on mowed plots [Turner, 1990], and was negatively related to NDVI early and late in the season on experimental plots and from June-July on grazed sites. In contrast, Dyer et al. [1991] showed that NDVI was positively related to %N.

N mass, a product of %N and grass biomass, was positively related to NDVI throughout the season on grazed sites (Table 3) and early in the season on experimental plots (Table 2). The difference in the nature of these relationships emphasizes the importance of biomass or leaf area in influencing single-time measurements of NDVI of tallgrass prairie. However, for the plot data pooled over sampling dates, a positive relationship ($R^2 = 0.19$, $P < 0.0002$, df = 66) between %N and NDVI is evident (Figure 6a). In contrast, biomass and NDVI values were not linearly related over the sampling period for either the plot data ($R^2 = 0.007$, $P = 0.52$, df = 67) or on grazed sites (Table 3).

Soil reflectance effects. Soil background conditions may strongly affect surface reflectance characteristics. Dry soils on KPRNA reflect more visible and less NIR radiation than green vegetation [Asrar et al., 1986]. Defoliation severe enough to expose the soil surface will also tend to decrease NDVI values and increase reflectance of visible light. For a given amount of vegetation, darker soils result in higher vegetation index values when these indices are based on ratios of NIR to red reflectance [Colwell, 1974; Elvidge and Lyon, 1985; Huete et al., 1985]. Reflectance of both visible and NIR wavelengths from bare KPRNA soils decreases as soil water content increases [Asrar et al., 1986]. Thus differences in soil moisture over the growing season and over the study site contributed to the spatial and temporal variation in NDVI and reflectances. The influence of exposed soil on reflectance measures also is affected by the dependence of soil reflectance on the optical properties of overlying vegetation [Jackson et al., 1980; Lillesaeter, 1982; Heilman and Kress, 1987; Huete, 1987]. The differential transmittance of red and NIR wavelengths through canopies [Kimes et al., 1985; Sellers, 1985; Choudhry, 1987] results in complex soil-vegetation interactions that are altered by defoliation. Vegetation indices are most sensitive to soil background influences in canopies with intermediate levels of cover [Huete et al., 1985], that is, over ranges observed in this study.

Senescent material. Reflectance from tallgrass canopies in all wavelength bands, except NIR, increases as plants mature and leaves become senescent [Asrar et al., 1986]. NDVI values decline over the growing season, partly owing to the accumulation of senescent material. On unburned sites, senescent vegetation from the previous year is present throughout the current growing season and may account for the higher reflectance of visible wavelengths and lower NDVI values observed in all seasons on unburned sites than on burned sites. On grazed sites, grass biomass may be consumed before it becomes senescent or removed from the canopy by the trampling action of cattle. This may result in a greater proportion of green material and an equal or higher NDVI value late in the season on grazed sites compared to unburned and burned sites (Figure 4).

Grazing versus Mowing

Experimental plots were used in part to minimize the effects of differences in site characteristics on plant responses and reflectance characteristics following defoliation. However, reflectance characteristics of experimental plots and grazed sites were similar in ways that suggest experimental plots were useful surrogates of grazed areas. Relationships between NDVI and canopy characteristics on experimental plots were similar to those on grazed sites early in the season when plant growth rates were high (Tables 2 and 3). Relationships vary with season regardless of mode of defoliation. Mowing and grazing increased reflectance of visible wavelengths and reduced reflectance of NIR wavelengths relative to undefoliated conditions in similar seasonal patterns. In addition, the magnitude of change in reflectance from undefoliated conditions for grazed sites most often approximated that for the moderate (10 cm) mowing regime.

Grazing-Landscape Interaction

Grazing interfered with the correspondence of biomass (and NIR/red vegetation index) to hill slope position found for ungrazed watersheds [Schimel et al., 1991; Davis et al., this issue]. The magnitude of this interference is expected to be a function of grazing intensity, with moderate grazing resulting in a patchy landscape (consisting of both grazed areas with low biomass and ungrazed areas with high biomass) and heavy grazing producing a more or less homogeneous canopy across watersheds.

Spatial variation in NDVI was higher on grazed sites than on burned sites. Variation in NDVI is highly scale dependent and on grazed sites may have been a function of grazing patch size. This pattern is, however, probably reversed at the landscape level because grazing removes the components of the variance contributed by topography and fire [Davis et al., this issue]. While it is impossible to estimate the amount of variability in satellite-derived NDVI values that might result from grazing based on measurements made with a ground-based radiometer, spatial patterns in remote sensing imagery probably are influenced by grazing patterns. Measures of landscape contrast using textural contrast algorithms [Jensen, 1986] have been related to impacts of tallgrass prairie disturbances [Nellis and Briggs, 1989] and may be useful in identifying grazing-induced spatial patterns.

These results complicate extrapolation of canopy characteristics and surface climate processes (such as surface fluxes) from point data to regions, such as the FIFE site. As an extrapolation method, biophysical stratification of grassland regions based on topography, soil type, and burning regime [e.g. Davis et al., this issue] may be improved by inclusion of grazing intensity. However, this information is difficult to obtain. Remote sensing may be the only feasible means for the assessment of surface properties affecting surface energy budgets and climate over large areas where grazing is an important land use.

Implications of Defoliation for Remote Sensing Studies

In studies of primary productivity and forage availability in grasslands, estimates of green biomass can be obtained from direct correlation of biomass with spectral reflectance [Waller et al., 1981; Weiser et al., 1986]. Field studies of agricultural crops and grasslands have shown a strong linear relation between intercepted photosynthetically active radiation (PAR) and spectral vegetation indices based on the ratio of NIR to red reflectance [Kumar and Monteith, 1982; Daughtry et al., 1982; Hatfield et al., 1984; Asrar et al., 1984; Weiser et al., 1986]. Thus, above-ground biomass can be estimated indirectly by estimating the fraction of absorbed PAR and computing biomass as a summation over time of converted PAR [Weiser et al., 1986; Kanemasu et al., 1989].

These methods assume that little change in biomass occurs between data acquisition and resource utilization and that the relationship between green biomass and spectral indices is not a function of stage of growth or regrowth. Results of this study demonstrate that (1) large increases in biomass (and NDVI) occur over relatively short periods following defoliation, (2) changes in N concentrations and allocation patterns following defoliation by grazers reduces the usefulness of NDVI as an indicator of biomass and leaf area, and (3) NDVI-biomass relationships may be season-specific, with sensitivity of this relationship minimized at midseason (Figure 6; see also Davis et al. [this issue], Dyer et al. [1991]).

Cattle are often attracted to the most productive sites (containing the preferred C_4 grass species) and frequently regraze such areas, thereby maintaining low plant biomass [Hobbs et al., 1991]. The net result of this activity is that neither fire management nor soil type (as a function of hill slope position) becomes a good predictor of plant biomass or leaf area index (LAI, Davis et al. [this issue]). Grazing tended to produce a more "homogenous grassland" in terms of surface energy flux [Smith et al., this issue] than would be predicted based on either physical site characteristics or LAI values.

NDVI-derived indices of LAI from ungrazed vegetation could be used to provide an index of plant/trace gas and plant/evapotranspiration (ET) relationships [Arkley, 1963]. However, management activities ubiquitous to grasslands, grazing, or mowing, severely limit the usefulness of NDVI-derived estimates of trace gas and latent heat flux. Still, procedures may exist to correct for underestimation of fluxes associated with grazed vegetation. Water-stressed or senescent vegetation tends to have warmer canopy temperatures owing to the relatively low ET rates of these surfaces in late summer [e.g., Asrar et al., 1988]. Canopy temperature was strongly negatively related to biomass (and LAI) on our experimental plots ($R^2 = 0.57$, $P = 0.001$, $df = 23$; see Figure 9a). This was caused in part by the reduction of transpiring leaf area by mowing. However, the increase in N concentration (an indicator of physiological activity) that results from foliage removal was also strongly related to surface temperature ($R^2 = 0.78$, $P = 0.0001$, df = 23; see Figure 9b). Accordingly, sensors that measure canopy temperatures could allow correction for a more physiologically active canopy that, owing to grazing or other variables, has a reduced LAI.

Implications of Defoliation for Surface Energy Budget Studies

Defoliation-induced changes in reflectance observed in this study suggest that net radiative input (R_n) is less on grazed sites. For the growing season, reflectance of visible radiation averaged 4-27% higher on mowed plots than on unmowed controls and approximately 8% higher on grazed sites than on burned but ungrazed sites. Thus, net radiative input in the visible portion of the spectrum was reduced by defoliation. Reflectance of NIR averaged 8-18% lower on mowed plots than on unmowed controls and approximately 15% lower on grazed sites than on burned sites. Thus net radiative input in this portion of the IR spectrum was increased by defoliation. However, increased soil exposure and concommitant increased soil temperature results in increased longwave export, leading to significant reductions in R_n [Smith et al., this issue]. Hence, grazing may alter surface energy budgets, through lower R_n and, via reduced leaf area, shifted partitioning of surface flux between latent and sensible heat fluxes. Analysis of surface energy budgets in relation to site management of the FIFE area is presented elsewhere [e.g., Smith et al., this issue; Davis et al., this issue]. Considering the different effects of sensible and latent heat flux (local warming of the atmosphere via sensible heat versus transport and release of energy downwind via latent heat flux), significant patterns in atmospheric circulation and local and regional climate may be driven by land use patterns that include grazing [Pielke and Avissar, 1990; Pielke et al., 1991].

Acknowledgments. We thank R. A. Ramundo for coordinating field data collection and for chemical analyses, J. M. Briggs for assistance in data analysis, and G. Asrar for providing equipment and technical assistance. Landscape data collection and analysis was assisted by J. Neubert, M. Lindquist, M. Nakada, and R. Hansen. The University of Nebraska FIFE research group provided MMR data. A. K. Knapp, D. C. Hartnett, and M. D. Nellis provided helpful comments on early versions of the manuscript. Support was provided by NASA grants NAG-5-897 and NAG-5-910 and NSF grants BSR-8514327 and BSR-89044632.

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TABLE 1. Results of ANOVA on the Effects of Mowing Height and Day of Year on NDVI and Coefficients of Variation of NDVI.

Variable	Treatment	df	F-value	P	r^2
NDVI	model	71	53.19	0.0001	0.94
	height	3	70.53	0.0001	
	day	12	83.78	0.0001	
	height x day	36	23.43	0.0001	
CV NDVI	model	71	1.72	0.001	0.34
	height	3	8.94	0.0006	
	day	12	2.01	0.02	
	height x day	36	1.47	0.05	

NDVI = Normalized Difference Vegetation Index, CV NDVI = coefficients of variation of NDVI. df, F-value, r^2 and P refer to the degrees of freedom, calculated values of the F statistic, the coefficient of determination and significance level, respectively, from an analysis of variance (ANOVA).

TABLE 2. Regression Equations for Relationships Between NDVI and Grass Nitrogen Concentration, Nitrogen Content of Grass Foliage, and Total Above-ground Plant Biomass on Grazing Intensity Experiment Plots.

Day of year	x	NDVI = $b_0 + b_1x$			r^2	P
167	%N	1.14	-	0.386x	0.62	0.0001
	N mass	0.49	+	0.117x	0.63	0.0001
	biomass	0.50	+	0.0011x	0.76	0.0001
243	%N	0.67	-	0.00015x	0.0002	0.99
	N mass	0.65	+	0.0052x	0.04	0.34
	biomass	0.65	+	0.00003x	0.08	0.18
301	%N	0.63	-	0.170x	0.43	0.0005
	N mass	0.50	+	0.017x	0.06	0.28
	biomass	0.47	+	0.00017x	0.35	0.004

Values for grass nitrogen concentration are given as %N; nitrogen content of grass foliage (N mass) and total above-ground plant biomass (biomass) are given in grams per square meter. b_0, b_1 and r^2 are the estimated slope, intercept and coefficient of determination, respectively from simple linear regression analysis. P is the significance level, indicating the usefulness of the regressor variable (x) as a predictor of NDVI. Degrees of freedom (df) are 19, 22, and 20 for days 167, 243, and 301, respectively.

TABLE 3. Regression Equations for Relationships Between NDVI and Grass Nitrogen Concentration, Nitrogen Content of Grass Foliage, and Total Above-ground Plant Biomass during 1987 on Sites Grazed by Cattle.

Period	x	NDVI = $b_0 + b_1x$			r^2	P
June - October	%N	0.639	-	0.0148x	0.001	0.98
	N mass	0.413	+	0.138x	0.41	0.003
	Biomass	0.538	+	0.0004x	0.12	0.15
June - September	%N	0.793	-	0.117x	0.15	0.13
	N mass	0.509	+	0.090x	0.28	0.04
	Biomass	0.581	+	0.0003x	0.15	0.14
June - July	%N	0.944	-	0.200x	0.47	0.03
	N mass	0.460	+	0.147x	0.72	0.001
	Biomass	0.583	+	0.0005x	0.40	0.05

Regressions were performed for data collected June - October (degrees of freedom = 18), June - September (degrees of freedom = 15), and June - July (degrees of freedom = 9). Units same as in Table 2. b_0, b_1, r^2 and P are defined as in Table 2.

TABLE 4. Regression Analysis of Live Above-ground Grass Biomass and Nitrogen Content of Live Above-ground Grass Material on Soil Depth for May 28-31, 1987.

Treatment/ Transect	Biomass on Soil Depth					N Content on Soil Depth				
	b_0	b_1	r^2	df	P	b_0	b_1	r^2	df	P
Ungrazed*										
1D	135	1.08	0.15	31	0.03	1.68	0.0206	0.25	31	0.003
UB	79	0.94	0.12	34	0.04	1.34	0.0202	0.14	34	0.02
N4	45	1.78	0.35	40	0.0001	0.56	0.0342	0.42	39	0.0001
2D†	140	0.79	0.12	28	0.06	1.61	0.0145	0.14	28	0.04
Grazed										
R5	NS		0.01	46	0.4	NS		0.00	46	0.7
R6	NS		0.01	28	0.6	NS		0.00	28	0.8

Form of the regression equations is: Biomass or N = $b_0 + b_1 \times$ Soil Depth. NS indicates regressions are not significant. Values for above-ground biomass (biomass) and nitrogen content of live aboveground grass material (N content) are given in grams per square meter; soil depth is given in centimeters. b_0, b_1, r^2, df and P are defined as in Table 2.

*Ungrazed transect identifiers refer to KPRNA research watersheds.

†Excludes 3 samples in sites disturbed by erosion or an old roadway.

Figure Captions List

Fig. 1. Mean NDVI versus day of year on (a) unmowed plots and (b) plots mowed once, (c) plots mowed three times, and (d) plots mowed six times during the 1987 growing season. Vertical lines indicate mowing dates. Plots in Figure 1d also were mowed on day 127. Error bars show standard errors.

Fig. 2. (a) Mean NDVI and (b) coefficient of variation of NDVI versus day of year on grazing intensity experiment plots for four levels of foliage removal. Control (ungrazed) plots are indicated by open circles, 5-cm foliage height by solid circles, 10-cm height by open squares, and 20-cm height by solid squares.

Fig. 3. Mean reflectance as a percent of mean reflectance on unmowed control plots versus day of year on grazing intensity experiment plots in four Exotech radiometer bands (a) B1, (b) B2, (c) B3, and (d) B4). Solid curve indicates 5-cm foliage height, dashed curve indicates 10-cm height, and dotted curve indicates 20-cm height.

Fig. 4. Mean NDVI versus day of year on grazed, burned ungrazed, and unburned ungrazed tallgrass prairie.

Fig. 5. Mean reflectance of ungrazed burned and grazed tallgrass prairie versus day of year in four Exotech radiometer bands (a) B1, (b) B2, (c) B3, and (d) B4. Solid curves indicate burned and dashed curves grazed sites. Error bars show standard errors.

Fig. 6. Relationship between NDVI and (a) percentage of N, (b) N mass, and (c) biomass on day 167 (pluses), day 243 (open circles) and day 301 (solid circles) during the 1987 growing season on grazing intensity experiment plots. Each point represents one plot. Lines are linear regressions. Dashed line in Figure 6a is for data pooled over sampling dates. For significance of slopes see Table 2 and text.

Fig. 7. Nitrogen mass of live above-ground grass material, live above-ground grass biomass, soil depth, and elevation above sea level along topographic transects in (a) ungrazed and (b) grazed watersheds for May 28-31 (FIFE IFC 1). Error bars show standard errors. Transect in Figure 7a ran west-east; that in Figure 7b ran east-west.

Fig. 8. Live above-ground grass biomass and N mass of live above-ground grass material as a function of transect distance and time (IFC's in 1987) for two grazed watersheds. Sample points and IFC dates are indicated by numbered posts.

Fig. 9. Relationship between surface temperature and (a) biomass and (b) %N on grazing intensity experiment plots. Each point represents one plot. Surface temperature was measured on day 196. Biomass was measured on day 243. Because plots were maintained at treatment heights there was little difference in biomass on days 196 and 243. Percentage of nitrogen was measured on day 190. Equations of the regression lines are $y = -0.025x + 48.46$ ($df = 22$, $r^2 = 0.57$) for biomass and $y = 16.60x + 23.68$ ($df = 22$, $r^2 = 0.78$) for %N.

Figure 1

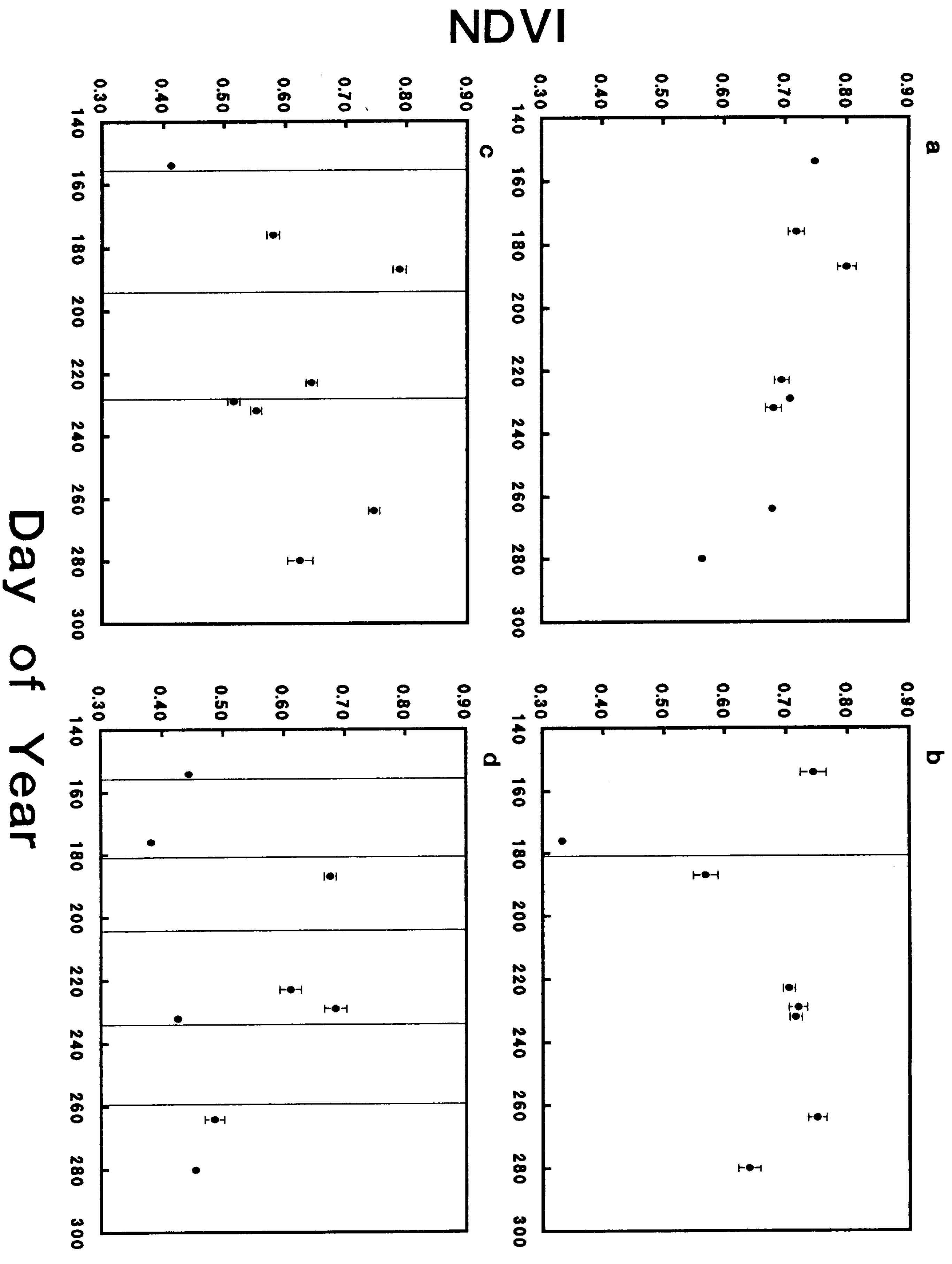

NDVI
Day of Year
a
b
c
d
0.30
0.40
0.50
0.60
0.70
0.80
0.90
140
160
180
200
220
240
260
280
300

Figure 2

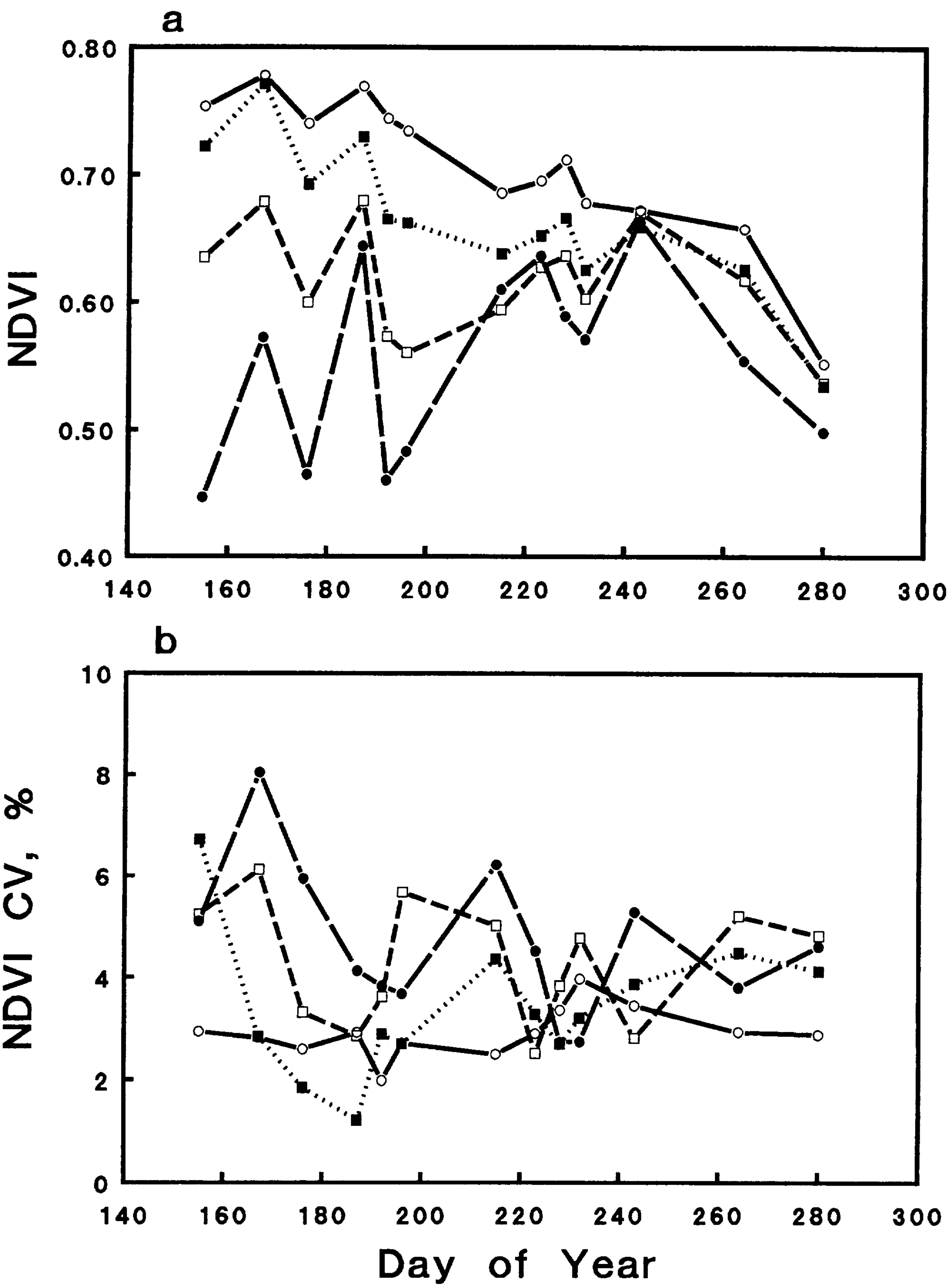

a
NDVI
0.80
0.70
0.60
0.50
0.40
140
160
180
200
220
240
260
280
300
b
NDVI CV, %
10
8
6
4
2
0
140
160
180
200
220
240
260
280
300
Day of Year

Figure 3

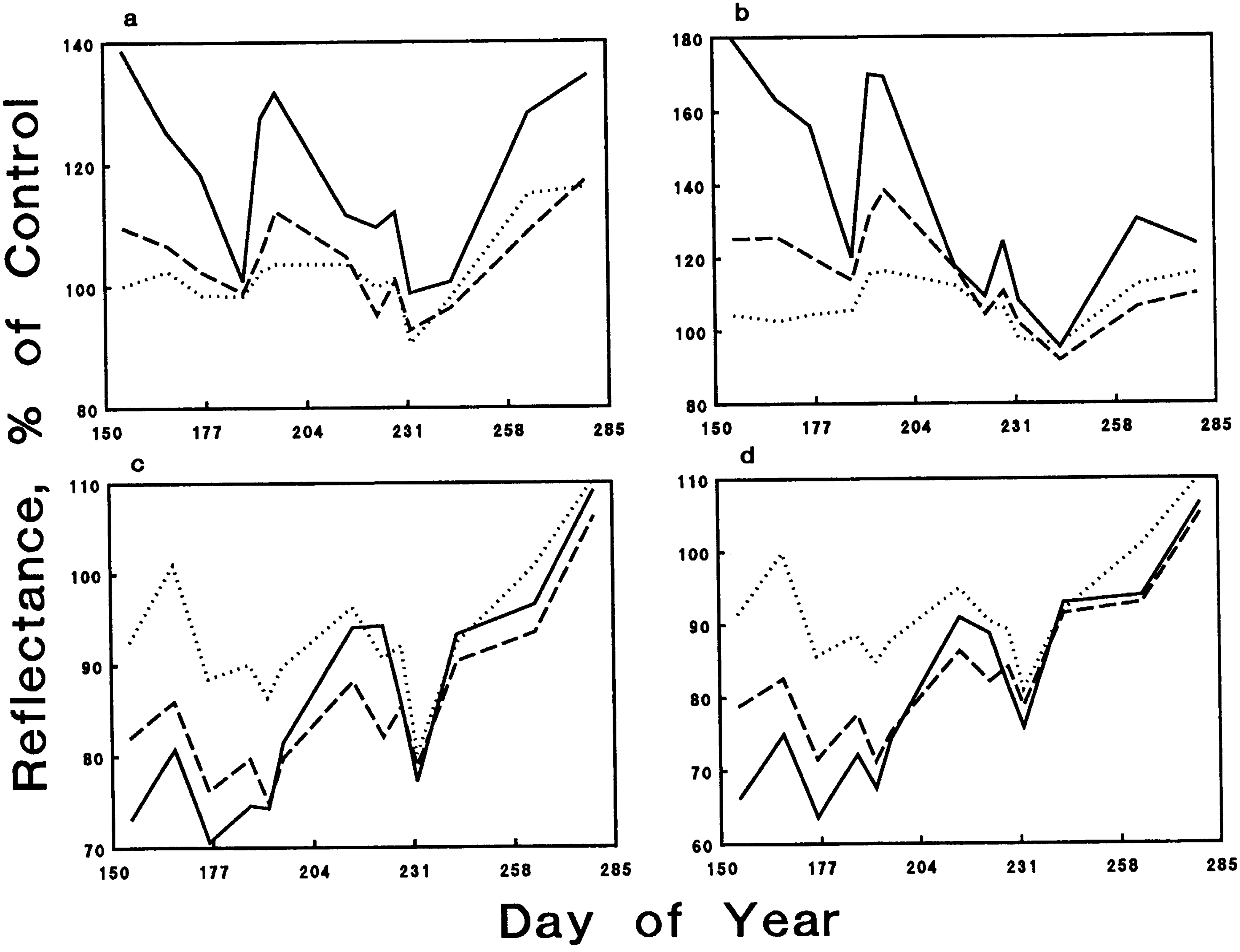

a
b
c
d
Reflectance, % of Control
Day of Year
140
120
100
80
180
160
140
120
100
80
110
100
90
80
70
110
100
90
80
70
60
150
177
204
231
258
285

Figure 4

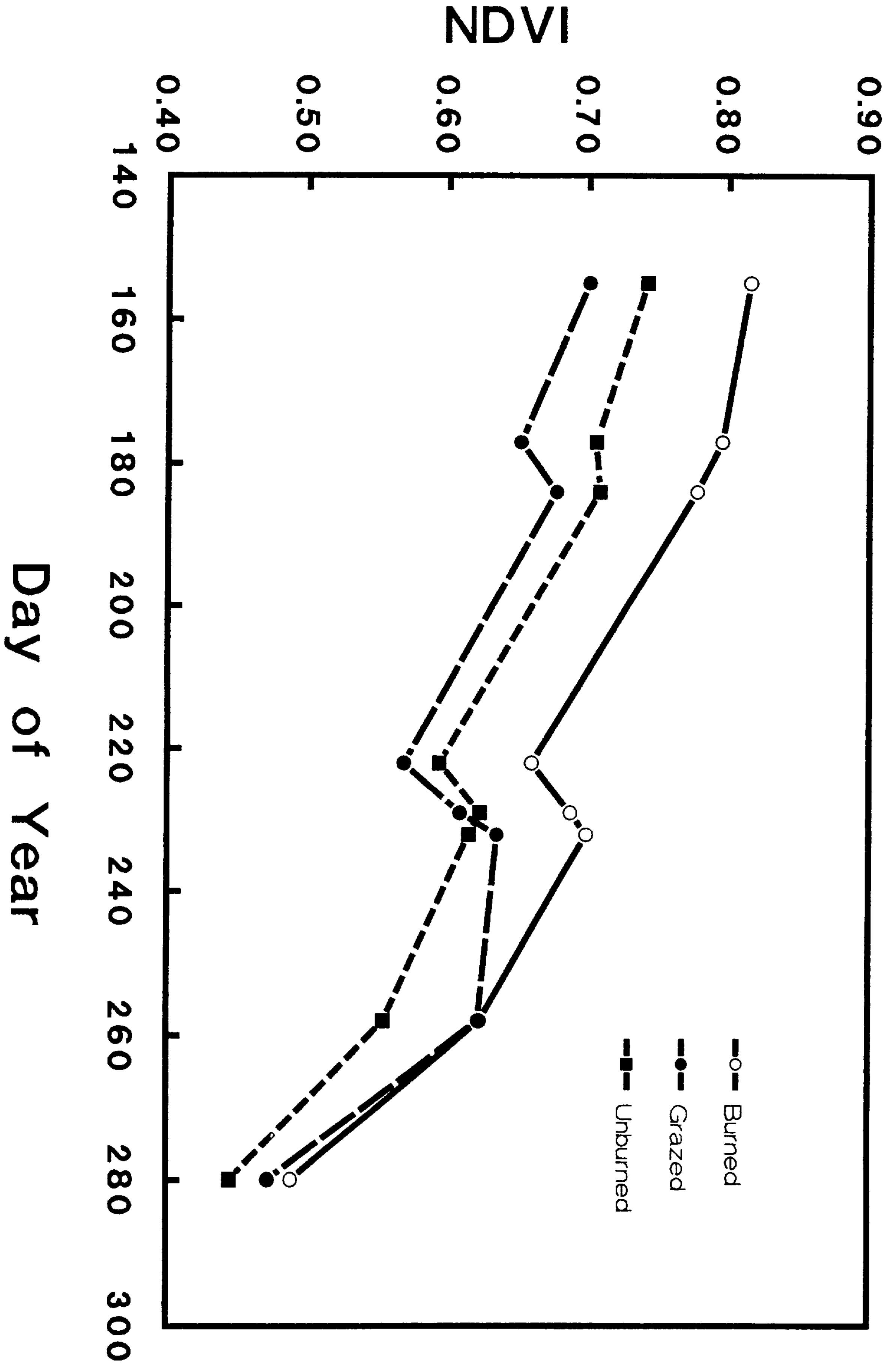

NDVI
0.40
0.50
0.60
0.70
0.80
0.90
140
160
180
200
220
240
260
280
300
Day of Year
Burned
Grazed
Unburned

Figure 5

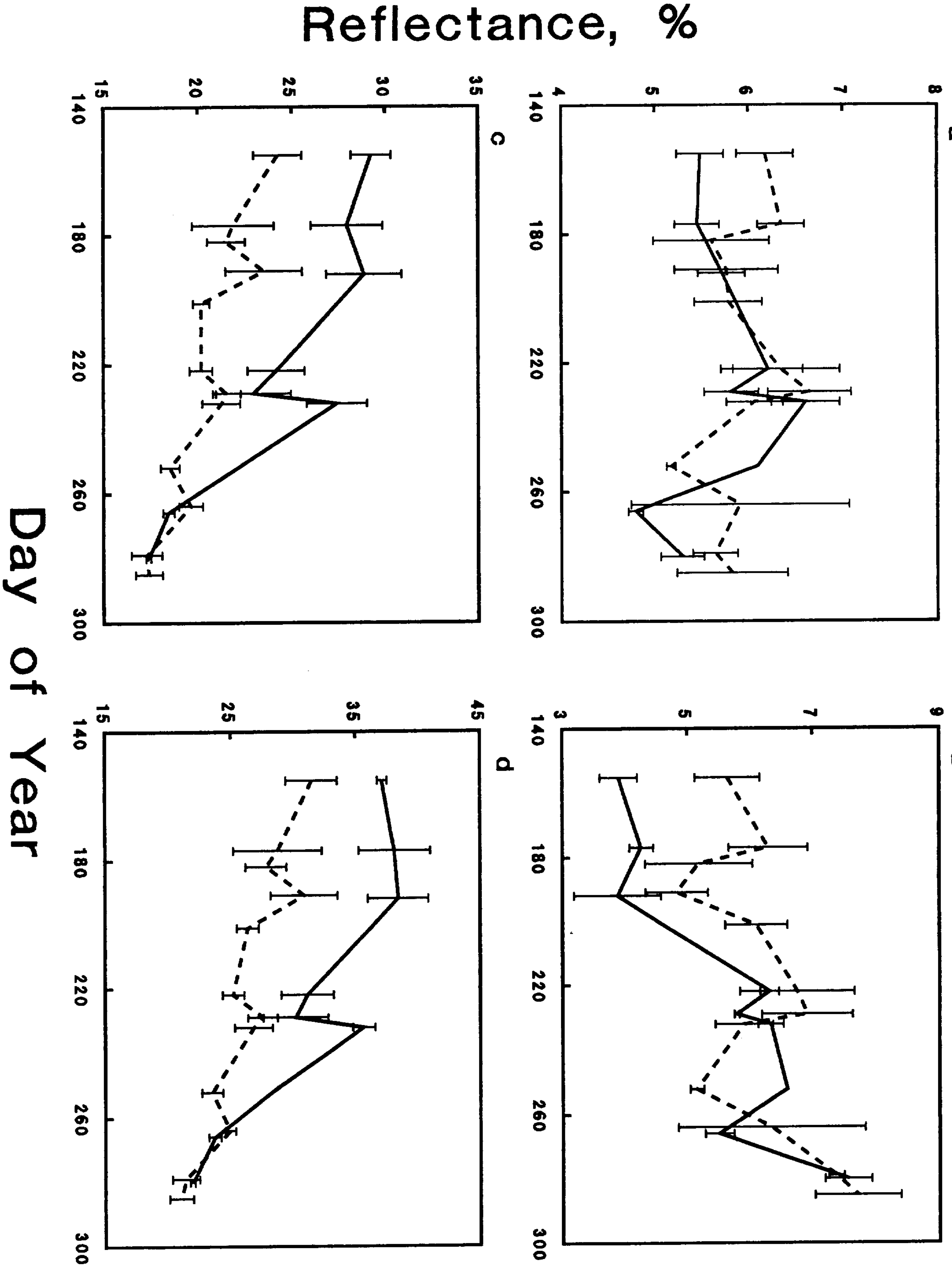

Reflectance, %
a
b
c
d
8
7
6
5
4
9
7
5
3
35
30
25
20
15
45
35
25
15
140
180
220
260
300
Day of Year

Figure 6

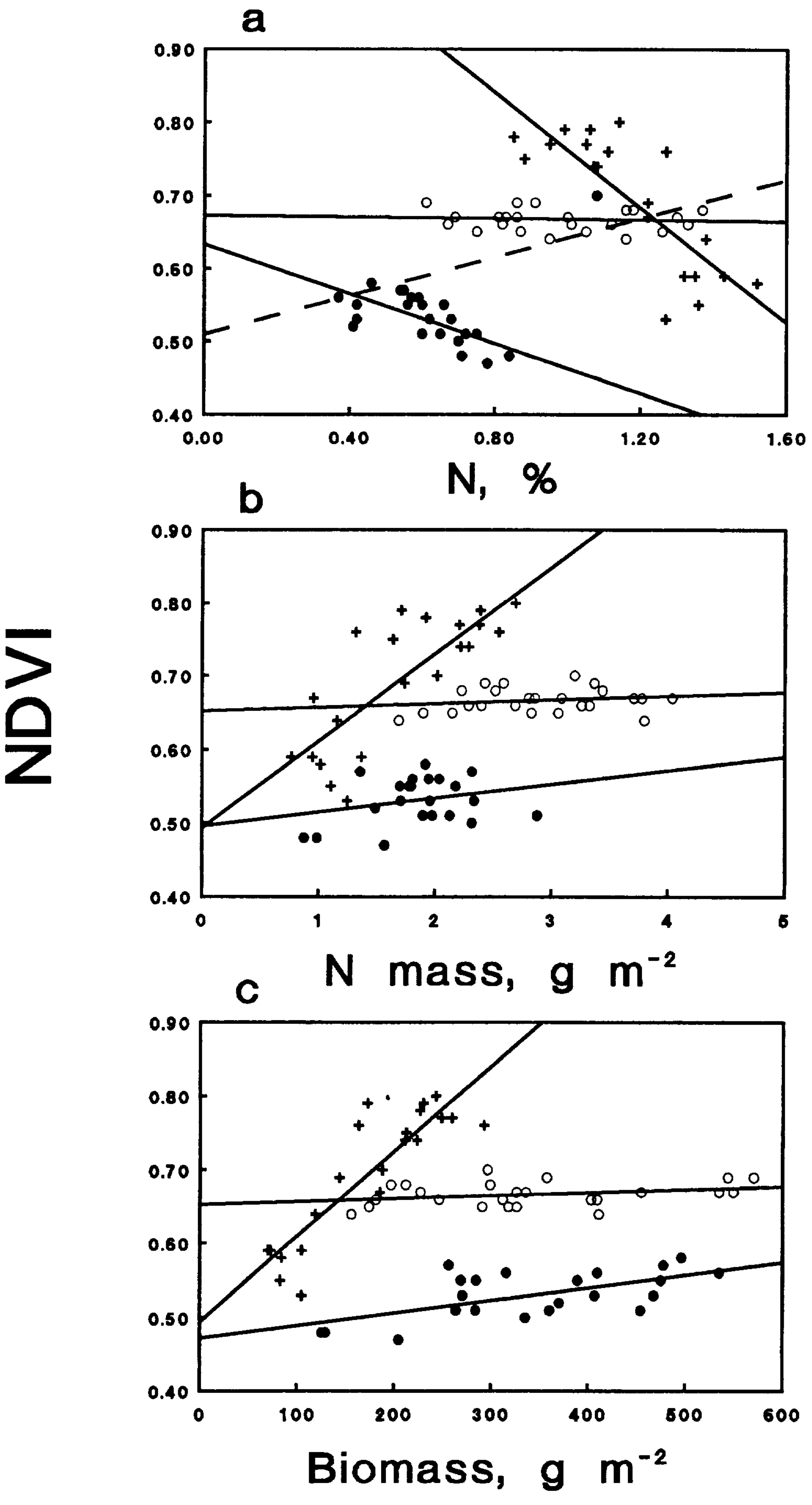

a
0.90
0.80
0.70
0.60
0.50
0.40
0.00
0.40
0.80
1.20
1.60
N, %
b
0.90
0.80
0.70
0.60
0.50
0.40
0
1
2
3
4
5
N mass, g m⁻²
c
0.90
0.80
0.70
0.60
0.50
0.40
0
100
200
300
400
500
600
Biomass, g m⁻²
NDVI

Figure 7A

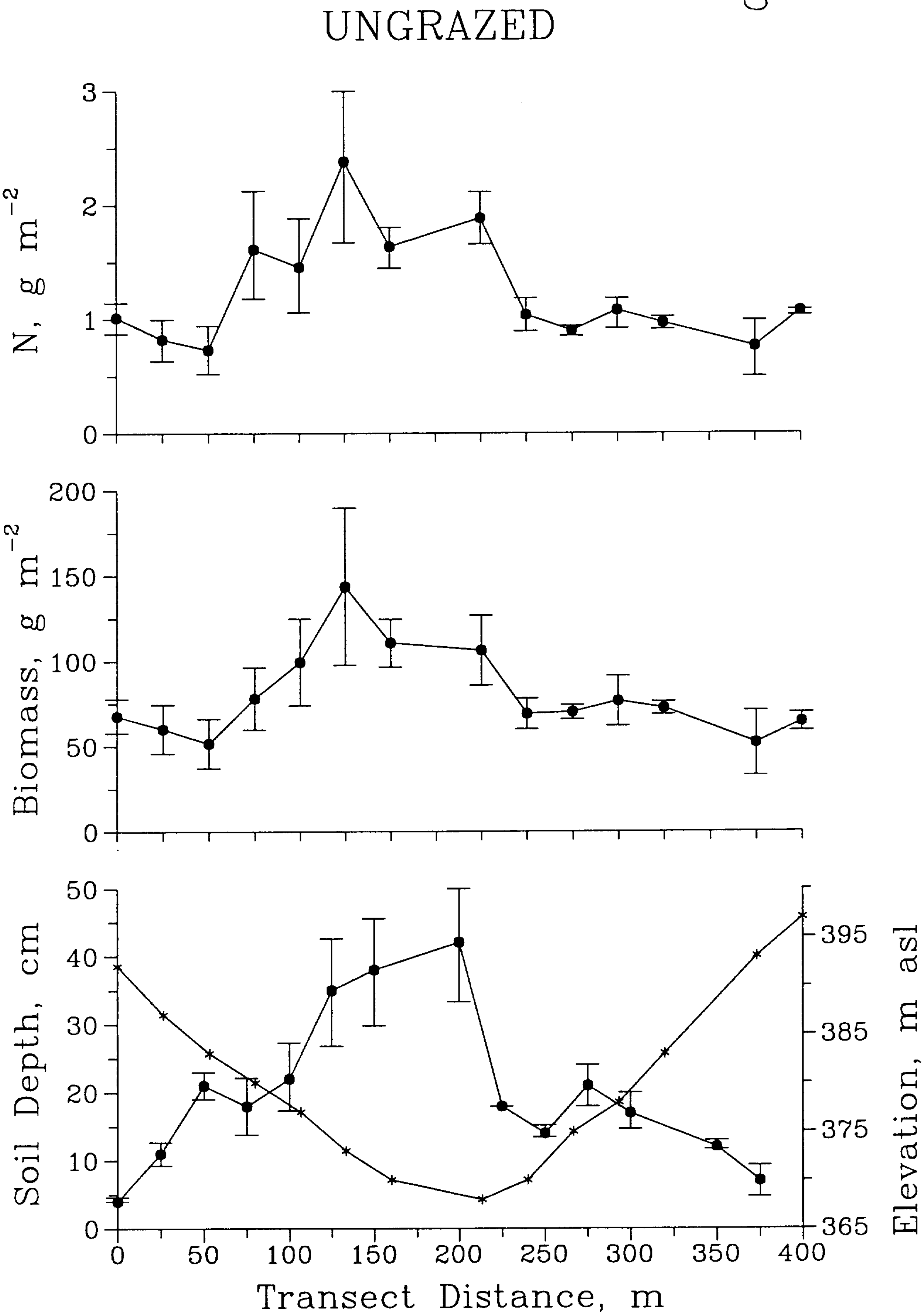

UNGRAZED
N, g m^{-2}
0
1
2
3
Biomass, g m^{-2}
0
50
100
150
200
Soil Depth, cm
0
10
20
30
40
50
Elevation, m asl
365
375
385
395
0
50
100
150
200
250
300
350
400
Transect Distance, m

Figure 7B

GRAZED

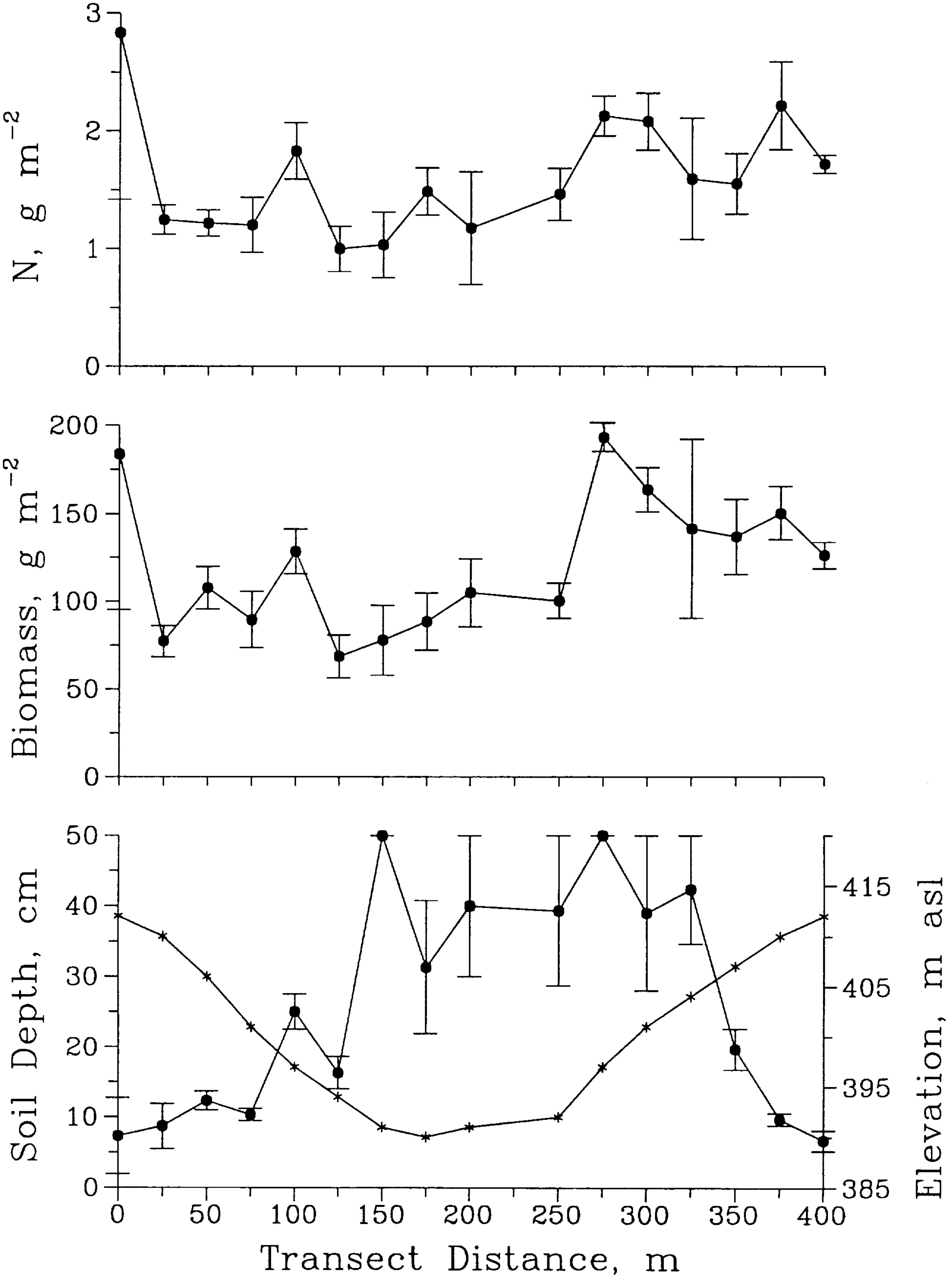
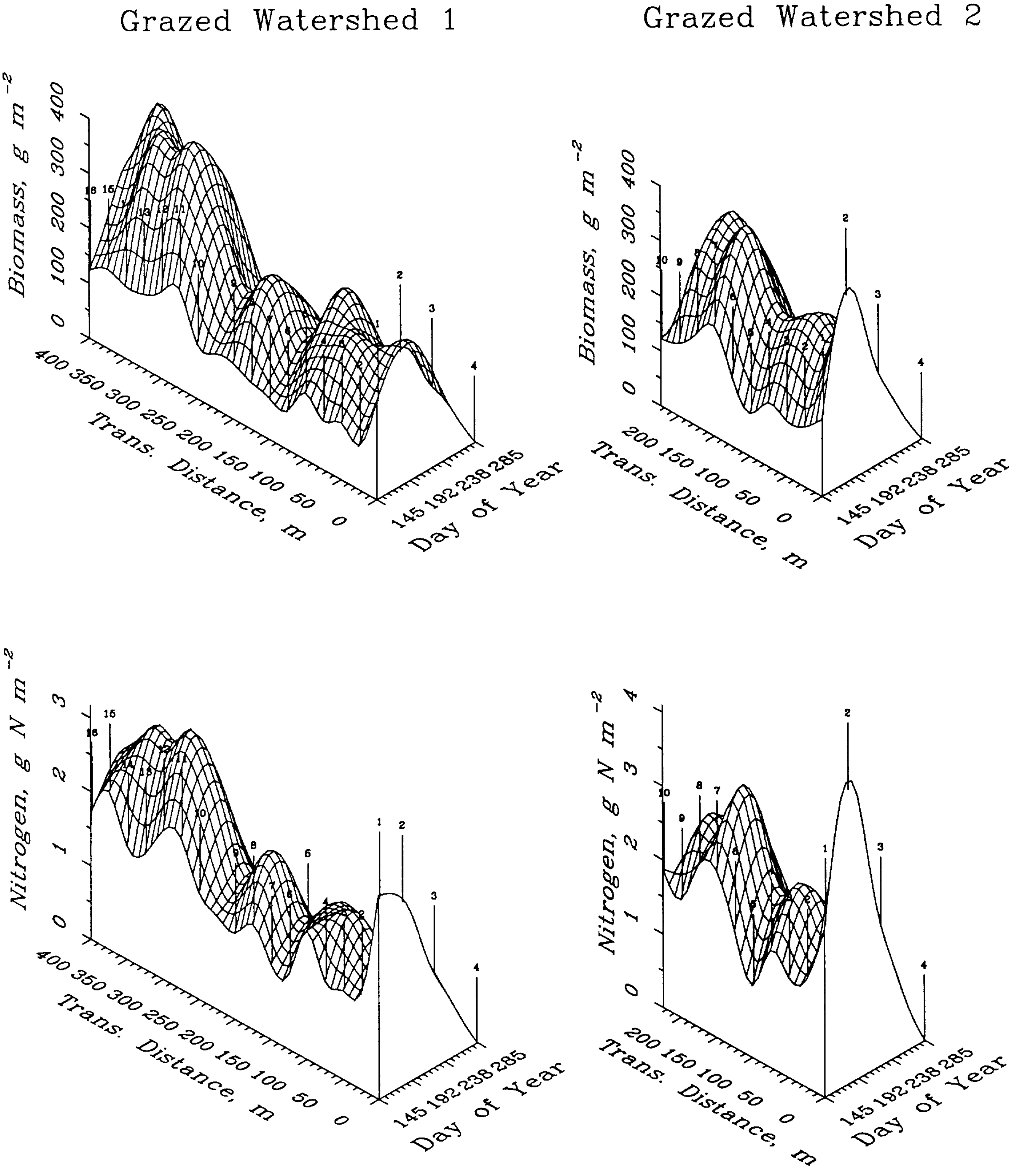
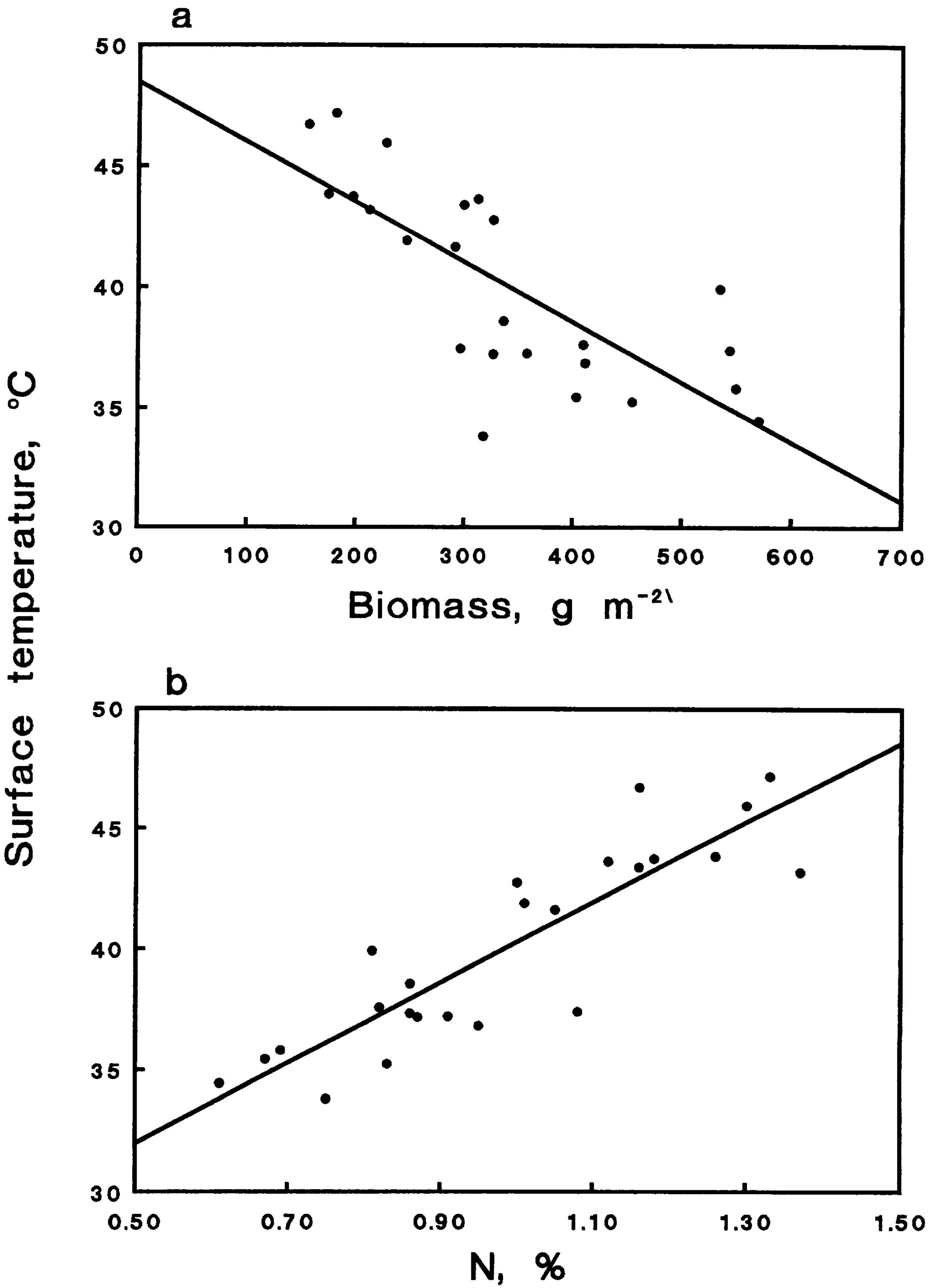


Figure 8



Grazed Watershed 1
Grazed Watershed 2
Biomass, g m $^{-2}$
0
100
200
300
400
Nitrogen, g N m $^{-2}$
0
1
2
3
4
Trans. Distance, m
400 350 300 250 200 150 100 50 0
200 150 100 50 0
Day of Year
145 192 238 285
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

Figure 9


a
50
45
40
35
30
0
100
200
300
400
500
600
700
Biomass, g m^{-2}\
Surface temperature, °C
b
50
45
40
35
30
0.50
0.70
0.90
1.10
1.30
1.50
N, %

MAXIMIZATION OF PRODUCTION IN GRASSLANDS

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MAXIMIZATION OF ABOVEGROUND PRODUCTION IN GRASSLANDS: THE ROLE OF DEFOLIATION FREQUENCY, INTENSITY AND HISTORY

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Submitted to: Ecological Applications

ABSTRACT

Production of tallgrass prairie vegetation was measured on experimental plots in which defoliation intensity and frequency were manipulated by mowing and using movable exclosures on areas chronically grazed by cattle. Defoliation history largely controlled whether or not defoliated plants overcompensated (exhibited enhanced production compared to undefoliated controls) for tissue removal. Plants on chronically grazed sites only compensated for foliage removed by grazers. Production on plots mowed prior to the year of measurement was similar to that on chronically grazed sites, while previously unmowed plots exhibited substantial aboveground overcompensation. Aboveground production was maximized by the most frequent mowing treatment and by intermediate mowing heights. Nitrogen and phosphorus concentrations and amounts in aboveground tissues were increased by mowing and grazing. Current mowing regime was more important than mowing history in determining nitrogen concentrations except very early in the growing season. Effects of grazing and mowing on belowground biomass were inconsistent, but frequent mowing appeared to limit accumulation of belowground N reserves and biomass.

In North American grasslands, overcompensation is a non-equilibrium plant response to grazing. Photosynthate that would be stored as reserves and used for root growth, flower and seed production instead is used to replace lost leaf area, thereby resulting in higher foliage productivity. However, under chronic grazing or mowing, vegetation is prevented from maintaining high nutrient and water uptake capacity (large root biomass) and accumulating reserves that allow overcompensation responses.

KEY WORDS AND PHRASES

tallgrass prairie; grazing by cattle; mowing; aboveground and belowground biomass; nitrogen; overcompensation; maximization of production; defoliation intensity, frequency, history

maximization responses in vegetation; belowground biomass responses to mowing frequency vs. mowing intensity; root biomass and long-term patterns of defoliation; grass production and N mass responses to mowing; chronic grazing and compensatory responses; carbon allocation to foliage following grazing; grazing history mediation of production maximization

INTRODUCTION

Much debate has focused on whether or not herbivory increases primary production (Belsky 1986, McNaughton 1986, Jeffries 1988) and on the ecological conditions (Georgiadis et al. 1989, Hartnett 1989, Maschinski and Whitham 1989) or level of biological organization (Brown and Allen 1989) in which increased production may occur. Results of several field and laboratory experiments suggest that primary production is increased by grazing (Dyer 1975, McNaughton 1976, Pearson 1965) even though herbivory is known to reduce biomass and production at the level of the individual tiller. For individual species, nutrient availability and interactions among weather, timing of herbivory and competitors, as well as species characteristics, determine responses to herbivory (Maschinski and Whitham 1989). At the ecosystem level, nutrient availability, as influenced by weather and the timing of herbivory, appears to be the primary control on productivity (Launchbaugh and Owensby 1978, Holland and Detling 1990).

A substantial data base on the aboveground response of grassland vegetation to grazing by livestock (Lacey and Van Poollen 1981, Sims and Singh 1978a,b) suggests that moderate grazing can have a positive, neutral or negative effect on primary production depending on the conditions of the study. McNaughton (1979) suggested that aboveground production is increased somewhat by low levels of grazing, reduced at very high levels of grazing, and maximized at some moderate level of grazing compared to production in the absence of grazing (the "grazing optimization hypothesis"). Overcompensation occurs when the amount of replacement biomass produced exceeds the amount removed by herbivores. Maximization of production at moderate grazing intensities is one example of overcompensation (McNaughton 1983).

Recently, Seastedt and Knapp (in review) reported that alternations in limiting resources produces consistent "maximization" responses in vegetation. These responses are observed over very short time periods (e.g., photosynthesis response to sunflecks), as well as over longer time intervals (e.g., production responses between years). In tallgrass prairie, equilibrium conditions, generated by the absence of fire and grazing, create energy limiting growth conditions caused by shading effects of litter (Knapp and Seastedt 1986). Plants and soils tend to accumulate nitrogen under these conditions. When energy constraints are removed or the strength of the aboveground sink for nutrients and photosynthate is increased, a greater than normal production response is possible due to higher than normal energy and nitrogen availability (Seastedt et al. 1991).

In the absence of grazing, the dominant tallgrass prairie vegetation tends to maintain large root systems and store substantial carbohydrate reserves in rhizomes (e.g. Rains et al. 1975). These reserves and the ability to acquire water and nutrients appear to allow rapid spring growth, with consequent shading of competing tillers. Reserves may also be used as an energy source for flowering stems, which are produced in early autumn in southern tallgrass zones. The availability of water may therefore control whether reserves are used for autumn flowering or for spring growth. These reserves may also be used for regrowth in the event of foliage or root destruction. Excellent reviews on carbon allocation responses of grasses are available (Marshall 1977), and recently Chapin (1991) has incorporated these and other studies in a generalized model of plant response to stress. Chapin noted that plants that divert resources to functions other than growth such as defense, storage or reproduction will lack the growth responses of species not allocating carbon and nutrients in this manner. From this perspective, grazing may result in increased production over the short term by inducing plants to use photosynthate for regrowth of aboveground tissue rather than for non-photosynthetic activities such as accumulation of reserves and maintenance of root systems. Under chronic grazing, however, plant production responses may be limited by lack of stored reserves or insufficient root biomass to supply demand for resources.

We hypothesized that overcompensation and the amplitude of the maximization response of grazed plants are largely controlled by storage of potentially limiting resources and the capacity to take up required resources from the soil prior to the initiation of grazing events. Preliminary evidence for the importance these stored reserves and belowground biomass came from the re-analysis of data reported 60 years ago by Aldous (1930, Fig. 1). This three-year study conducted on land previously lightly grazed indicated a modest overcompensation (117% of controls, using the fitted curve shown in Fig. 1) response to clipping in the first year, while the same clipping intensity had negative effects in the second and third years (Fig. 1). Plant responses changed dramatically through time, but the indirect effects of grazing (trampling, urine deposition, etc.) were not included or evaluated by that study.

In the present study we evaluated the role of grazing history on plant responses and compared the effects of the frequency and intensity of defoliation on plant responses of native tallgrass prairie. Grazing intensity was defined as the amount of leaf area remaining following defoliation and was manipulated experimentally by mowing at several heights. Grazing frequency was defined as the number of times foliage removal occurred and included grazing and mowing history as well as current mowing frequency. Observational studies also were conducted using moveable exclosures (McNaughton 1979) on long-term grazed pastures to provide data on actual grazing for comparison with results from mowed plots. This study was part of a larger effort to assess the effects of defoliation and fertilization on production and spectral reflectance properties of tallgrass prairie plant communities (Dyer et al. 1991, Turner et al., in press).

METHODS

Research was conducted on Konza Prairie Research Natural Area (KPRNA), a 3,487 ha site located about 12 km south of Manhattan, Kansas, in the Flint Hills of northeastern Kansas and on 5 other sites within 10 km selected for intensive study during the First International Satellite Land Surface Climatological Project (ISLSCP) Field Experiment (FIFE, Sellers et al. 1988). Dominant vegetation of this area is characterized by warm-season, tallgrass prairie species such as big bluestem (Andropogon gerardii Vitman), little bluestem (A. scolparius Michx.) Indian grass (Sorgastrum nutans (L.) Nash), and switchgrass (Panicum virgatum L.). A general description of the vegetation of this specific region of the tallgrass prairie is presented in Hulbert (1986), Bragg and Hulbert (1976) and Freeman and Hulbert (1986), while productivity of this region has been extensively documented for both grazed (e.g. Owensby et al. 1970, Launchbaugh and Owensby 1978) and ungrazed prairie (Towne and Owensby 1984, Briggs et al. 1989). Hobbs et al. (1991) provided recent information on the interaction of grazing and fire in the nitrogen dynamics of tallgrass prairie.

In 1987, a mowing intensity experiment was superimposed on 24, 10m x 5m plots established in early 1985. Previous to experimental treatments initiated in 1985, the site had not been grazed for 10 years. The site had been frequently burned in spring during this interval. One third of each plot was mowed 6 times during the growing season in 1985 and 1986, one third was mowed 3 times, and one third was left unmowed during 1985 and 1986. In 1987, these plots were used to create six replicates of the following mowing treatments: 1) unmowed (control), 2) mowed to 5 cm above ground level, 3) mowed to 10 cm, and 4) mowed to 20 cm. Mowing was conducted as needed to maintain vegetation at treatment heights and all plots were mowed on each sampling date. In 1987, all three sections of each plot were sampled until 7 June; only the sections that were previously unmowed and those mowed 6 times were sampled thereafter. Vegetation above the established experimental heights was clipped in one 0.1m^2 quadrat on each plot or section of plot just prior to mowing to estimate the amount removed by mowing. Vegetation in 0.1m^2 quadrats on each plot or section of plot was clipped to ground level on 16 June, 31 August, and 28 October. Aboveground biomass production was calculated for each plot by summing the estimates of biomass removed by mowing and the standing crop at each date. Mass of N and P incorporated into aboveground tissues was calculated by multiplying percent concentration and biomass and summing the result.

A separate mowing frequency experiment, also conducted in 1987, evaluated the consequences of complete foliage removal once, three times, or six times at regular intervals over the growing season. None of the plots used in this mowing frequency experiment had been mowed or grazed for 10 years. Plots were located adjacent to mowing experiment plots and were burned on the same schedule as intensity experiment plots. The mowing frequency experiment consisted of twelve 10 m x 5 m plots and eight 10 m x 10 m plots randomly assigned to create 5 replicates of the following mowing treatments: 1) unmowed (control), 2) mowed 1 time, 3) mowed 3 times, and 4) mowed 6 times during the growing season. All plots were mowed as close to the soil surface (approximately 2 cm) as possible. Aboveground standing crop was sampled by clipping at ground level in one 0.1 m^2 quadrat per plot just prior to mowing. Foliage biomass, N and P masses were calculated as before.

In 1987 and 1988, ten, 1 m x 1 m x 0.5 m high moveable cattle exclosures were used to quantify aboveground plant biomass dynamics on each of four sites. Three of these sites were located in uplands and were sampled each year. The fourth site sampled in 1987 was located on a moderate, north-facing slope. The fourth site sampled in 1988 was located on a steep south-facing slope. All sites had been grazed each year and burned frequently during the preceding 10 years.

Vegetation was sampled at 2-3 week intervals during the growing season by clipping all vegetation within 0.1 m^2 quadrats to ground level. Biomass was measured inside moveable exclosures, outside exclosures (in unprotected vegetation), and inside permanent exclosures. Exclosures were moved to previously unsampled locations within a distance of 10 m after samples were obtained, and these remained in place until the next sampling date. Net aboveground primary production since the last sampling date was calculated as the difference between mean plant biomass inside exclosures on the sampling date and mean plant biomass outside exclosures on the previous sampling date. Grass biomass consumed since the last sampling date was calculated as the difference between grass biomass inside and outside the exclosure. Estimates of cumulative production or consumption were calculated as the sum of positive differences from moveable exclosure data or the sum of positive biomass increments from permanent exclosure data. Statistically, this procedure may be biased (e.g., Singh et al. 1984); however, since relative growth rates of regrowth vegetation differ drastically from that of ungrazed vegetation (Hilbert et al. 1981; Vinton 1990), we believe this procedure is superior to using data from fixed, ungrazed exclosures.

Mass and N content of roots and rhizomes on the 1985-86 mowed plots were estimated in October 1986. Roots were collected using 5 cm dia. x 30 cm deep soil core samples; rhizomes were collected by hand-sorting 0.33 m by 0.33 m by 0.1 m deep soil monoliths. In October 1987, two soil cores (5 cm dia. by 20 cm deep) with roots and rhizomes intact were obtained from each experimental plot and from 4 locations at each grazed site. Each pair of cores were composited into one sample. Four paired cores also were obtained from an additional 9 ungrazed and 2 grazed sites. While grass rhizomes were collected in soil cores, the small size of the samples, in conjunction with a tendency for live rhizomes to break rather than cut cleanly in the coring tool, prevented this procedure from producing accurate estimates of rhizomes. Only root data are therefore reported from the soil core samples. Plant material was separated from soil using methods described by Smucker et al. (1982), as modified by Hayes and Seastedt (1987).

All aboveground plant material was sorted into grasses and forbs, dried at 60 degrees C to constant mass, and weighed. Belowground plant material was sorted into live and dead grass roots, forb roots and rhizomes, dried, and weighed. Dried grass samples were ground through a 40-mesh screen, digested with a micro-Kjeldahl procedure and processed through a Technicon Autoanalyser for total nitrogen and phosphorus.

Effects of mowing intensity and frequency on foliage production, nutrient concentration, and belowground biomass were analyzed using one-way analysis of variance. N and P concentration data were transformed using an arcsine-square root transformation (Zar 1984) before analysis. Effects of previous mowing frequency and mowing intensity on production, nutrient concentration, and belowground biomass were analyzed using two-way analysis of variance.

RESULTS

Precipitation for 1987 was 94% of average. June was drier (16% of average) and August was wetter (240% of average) than the 35-year mean for those months. Growing season precipitation (April - September) was 92% of average. In 1988, precipitation was 58% of average for the year and 66% of average for the growing season. Thus, the study period included both nominal and drought conditions.

Root and Rhizome Biomass

Belowground biomass at the end of the 1986 growing season, and consequently the initial conditions of intensity experiment plots, were affected by mowing in 1985-86 (Table 1). Autumn 1986 live grass root biomass was significantly reduced by mowing ($F = 3.91$, $P < 0.04$), with reductions of approximately 30% compared to unmowed plots resulting from mowing 6 times. N mass in live rhizomes also was reduced by mowing ($F= 3.33$, $P < 0.05$). Mowing had no effect on dead root biomass, dead rhizome biomass or the amount of N in these parts.

Autumn 1987 total root biomass to a depth of 20cm ranged from 813 to 1456 g m^{-2} for all sites sampled in this study. Grass root biomass (live + dead) comprised over 91% of total belowground biomass at each site. The ratio of dead to live grass roots ranged from 2.9 to 6.6 and averaged 4.5. Forb (herbaceous dicot) root biomass comprised less than 10% of total root biomass at all sites.

Analyses of variance indicated that there were no statistically significant effects of grazing, mowing height or frequency, or previous mowing history on end-of-season total root biomass or any component of root biomass (total grass roots, live grass roots, dead grass roots, and forb roots). However, trends in root biomass data from the intensity experiment were related to long-term patterns of defoliation (Fig. 2A). Live grass root biomass was less on plots mowed in 1985-86 than on plots never mowed, and the reduction in biomass was not related to mowing height. Dead grass root biomass was 14-29% greater on mowed plots than on unmowed controls, and dead root mass was consistently higher on plots mowed in 1985-86 than on same treatment plots left unmowed during this time. Live and dead root N concentrations were not affected by mowing height. Consequently, N mass in these tissues showed the same patterns as did biomass.

Mean grass root biomass on 3 types of sites in this study (first year of grazing, long-term grazed, or long-term ungrazed) appear in Fig. 2B. Data for the first year of grazing were from plots mowed 6 times in the mowing frequency experiment and intensity experiment plots unmowed in 1985-86 and mowed to 5cm in 1987. Effects of length of grazing on root biomass were not statistically significant but the data suggest that root production is lower in the first year of grazing than on sites with long histories of grazing or the absence of grazing.

Aboveground Response on Plots with No Recent History of Grazing:

Mowing Frequency

An ANOVA indicated that mowing frequency significantly affected season-long grass production ($F = 6.92$, $P < 0.004$). Production increased with mowing frequency (Fig. 3). Mean biomass production on plots mowed 1, 3, and 6 times was 19, 38, and 61, percent greater, respectively, than on unmowed plots. Forb production accounted for approximately 6 percent or less of total aboveground production and was not affected by mowing frequency.

Mowing frequency also affected aboveground N and P mass ($F = 50.76$, $P < 0.0001$; $F = 22.67$, $P < 0.0001$, respectively, Fig. 4). Nitrogen mass on plots mowed 1, 3, and 6 times was 1.7, 3.3 and 4.3, times greater, respectively, than on unmowed plots. Phosphorus mass on plots mowed 1, 3, and 6 times was 2.1, 3.8, and 5.2 times greater, respectively, than on unmowed plots. Mowing resulted in elevated foliar concentrations in grasses of both N and P throughout the growing season compared to concentrations on unmowed plots. High initial tissue concentrations (2.4% N and 0.26% P on unmowed plots declined with early season growth to 0.85% N and 0.10% P by day 175 and remained low throughout the rest of the season. In contrast, foliar N and P concentrations on mowed plots was high (1.30-1.64% N and 0.16-0.20% P) until mowing was discontinued. Following retranslocation prior to senescence late in the season (Hayes 1985) concentrations were higher on mowed plots than on unmowed plots (0.53% N and 0.06% P on unmowed plots vs. 0.65-0.99% N and 0.08-0.16% P on mowed plots).

Aboveground Response on Plots with No Recent History of Grazing:

Mowing Intensity

Differences in aboveground grass production due to cutting foliage to different heights were not statistically significant early in the season (day 167, $F = 0.20$, $P < 0.89$). However, plots mowed to 5, 10, and 20 cm heights had produced on average 6, 14, and 17 percent, respectively, more grass biomass than had unmowed controls (Fig. 5A). By day 243, all mowed plots had significantly outproduced unmowed controls ($F = 5.35$, $P < 0.007$), with 5, 10, and 20 cm plot producing 32, 42, and 54 percent, respectively, more than unmowed controls. Biomass increased on control plots but not on mowed plots after 31 August (day

243). As a result, differences between treatments at the end of the growing season were not significant (day 301, $F = 2.60$, $P < 0.08$). By the end of the growing season, however, 5, 10, and 20 cm plots had produced on average 13, 21 and 26 percent more than unmowed controls. Forb production was highly variable within and between treatments. Forbs and accounted for 7-12% of annual aboveground production. There was no evidence for increased forb production due to reduced competition from grasses. The ephemeral nature of many tallgrass prairie forb species and the sampling scheme employed in this study make it unlikely that competitive release would be observed.

Tissue removal resulted in increased nutrient concentrations and amounts of nutrients in aboveground tissues in direct relation to the intensity of mowing. By late August (day 243) N mass in aboveground tissue was significantly higher ($F = 16.95$, $P < 0.0001$) for all mowing heights than on unmowed controls (Fig. 5B). N mass was approximately 2.2 - 2.5 times higher on mowed plots than on unmowed plots. At the end of the growing season differences between mowing treatments and unmowed controls were significant (day 301, $F = 18.83$, $P < 0.0001$). N amounts were not as large as at the August sampling date perhaps because of retranslocation of N to belowground organs after midseason (Hayes 1985). Nitrogen and P concentrations in aboveground tissues declined over the growing season under all treatments. Nitrogen concentrations were affected by mowing height at every sampling date after day 141 (ANOVA by date, $P < 0.05$ for 7 dates). Phosphorus concentrations also were affected by mowing height on all sampling dates after day 141, except day 175 (ANOVA by date, $P < 0.05$ for 6 dates).

Foliage Response of Sites with History of Defoliation:

Historical Mowing Frequency

Early in the growing season (to day 154), grass removed by mowing ~~on~~ plots mowed ~~in~~ 1985-86 was significantly less than that harvested from plots left unmowed in 1985-86 (Fig. 6). Results of a two-way ANOVA of the effects of mowing height in 1987 and mowing frequency in 1985-86 indicated that reduced offtake was related to mowing history but not current mowing height and that there was no interaction between mowing history and mowing height (F = 3.02, P < 0.01). Harvest amounts from plots mowed 3 and 6 times were little different, suggesting that, similar to Aldous's findings (Fig. 1), removal of foliage in one year significantly reduces subsequent growth.

Patterns of production resulting from differing defoliation intensities were clearly a function of the mowing regime in effect prior to this study (1985-86, Fig. 7). On previously unmowed plots, mowing resulted in greater production than on unmowed controls, regardless of mowing height, with light defoliation intensity (20cm mowing height) resulting in maximum production. On plots that had been mowed in 1985-86, production was reduced overall and maximized at an intermediate level of defoliation (10cm mowing height). Results of a two-way ANOVA using mowing height and history suggested that mowing history was more important than current mowing height in determining grass production well into the current growing season (Table 2). By day 310, both mowing history and intensity affected production significantly. Regression analyses of belowground biomass and N amounts at the end of 1986 on aboveground production in 1987 indicated significant but weak relationships. Season-long aboveground grass production and N mass in grasses were linearly related to N reserves (F = 5.68, $P < 0.02$, df = 31, $r^2 = 0.16$ for grass production and F = 5.48, $P < 0.03$, df = 31, $r^2 = 0.15$ for N mass). Season-long aboveground grass production was also linearly related to live grass root biomass (F = 4.93, $P < 0.03$, df = 31, $r^2 = 0.14$).

In contrast, mowing history was less important in determining N concentrations in foliage than was current mowing height. Only early in the growing season (day 141) were there significant differences in N concentrations due to previous mowing (Table 3). In addition, significant differences in concentrations due to mowing height at day 141 were not consistent with the pattern established later. After day 154, N concentrations were affected by current mowing height but not by previous mowing, with N concentrations decreasing with increasing mowing height.

Foliage Response of Sites with History of Defoliation:

Long-term grazed pastures

Grazing intensity varied widely both within and between seasons and sites (Fig. 8A, B). Standing crop of grasses was inversely related to grazing intensity in both years (Fig. 8C, D). In the drought year (1988), standing crop of grasses was much lower throughout the season than in 1987. In 1987, grasses at all sites except one appeared to compensate for foliage removal by grazing in direct proportion to the amount of foliage removed (Fig. 8E). Compensation resulted in season-long production similar to that on ungrazed plots despite large differences in the proportion of production removed by cattle. Continuous competition from a very diverse community of forbs may have prevented a compensatory response by grasses at the site that was the exception. In 1988, grasses at all sites except one appeared to compensate for foliage removal by grazing (Fig. 8F). Grass production on these sites was not different from production of grasses protected from grazing within a permanent exclosure.

Seasonal trends in nitrogen concentrations were directly related to grazing intensity in 1987 and 1988. In 1987 high early season N concentrations were diluted as grass biomass accumulated in ungrazed grasses and remained low for much of the growing season. In contrast, N concentrations on sites where 25% or more of production was removed was higher than that in ungrazed grasses throughout the growing season. In 1988, N concentrations were higher on heavily grazed sites than on sites where grazing was less severe.

In 1987, the amount of N incorporated into aboveground grass tissue on grazed sites ranged from 2.17 to 4.69 g m^{-2} compared to a mean of 2.25 g N m^{-2} (std error = 0.29, n = 3) at the end of the growing season in grasses protected from grazing in permanent exclosures. In 1988, the amount of N incorporated into aboveground grass tissue on grazed sites ranged from 2.33 to 3.45 g N m^{-2} compared to 2.06 g N m^{-2} (std error = 0.29, n = 2) at the end of the season in grasses protected from grazing. Peak (midseason) aboveground N in grasses protected from grazing was 4.14 g m^{-2}.

DISCUSSION

A variety of mechanisms have been proposed to account for increased production following grazing. Direct mechanisms primarily involving physiological responses of individual plants to defoliation include 1) increased photosynthetic rates in remaining tissue, 2) allocation of proportionately more photosynthate to the production of new leaf area, 3) increased tillering, 4) translocation of reserves from belowground organs to foliage, and 5) increased nutrient uptake by roots. Indirect mechanisms primarily involving alteration of resource levels following defoliation include 1) opening of the canopy and increased light penetration, 2) reduction in transpirational water loss because of reduced leaf area and conservation of soil water, and 3) more rapid cycling of nutrients by deposition of utilizable forms in fecal matter and urine in the upper soil layers (Botkin et al. 1981).

Our results demonstrate that defoliation history is of major importance in determining the magnitude of the aboveground "maximization response", and that, consistent with our hypothesis, chronic grazing fails to produce little more than a compensatory response. On plots not grazed for 10 years, grasses under all mowing treatments overcompensated for foliage removal when compared with unmowed controls. Aboveground production was 19-61 percent greater following mowing to ground level and 13-26 percent greater following maintenance at specific heights than production on unmowed plots. In contrast, aboveground production was generally less or no different on grazed sites in 1987 and 1988 than on ungrazed sites despite a range of grazing intensities similar to those imposed on treatment plots. Other studies of production on long-term grazed areas also suggest that chronic grazing limits the magnitude of the aboveground maximization response. For grazed and protected rangelands in the western U.S. Lacey and Van Poollen (1981) concluded that on average production of grazed areas was 68 percent lower than that of protected areas. Data from tallgrass prairie included in their review (Sims et al. 1978) indicated production of grazed areas was between 5 and 13 percent less than that on protected areas. Vinton (1990) reported reduced relative growth rates, biomass, and survival for individual tillers in the year following defoliation. In the year of defoliation, however, these tillers exhibited increased relative growth rates compared to undefoliated tillers and compensated for tissue removed.

Our 1987 data indicate that grazing does not have substantial negative impacts on root biomass, at least in the top 20 cm of soil. The data indicate a statistically nonsignificant decline after the start of grazing and that this reduction (relative to ungrazed) may be greater in the first year of grazing than on long-term grazed sites (Fig. 2). A strategy of allocating a disproportionately high percent of available photosynthate to replacing lost foliage at the expense of root production may be advantageous in the first year of grazing or if grazing occurs infrequently. Over the long term, however, a more equitable balance between above- and belowground production may be more advantageous. Our failure to show significant declines also may be an artifact of the sampling depth, as grazing influences root distribution as well as productivity (Lorenz and Rogler 1967). A large data base indicates that grazing consistently reduces root production and root biomass (Weaver 1950, 1958), although several studies have reported similar root biomass inside and outside grazing exclosures (Sims and Singh 1978a, b, Milchunas and Lauenroth 1989, van der Maarel and Titlyanova 1989).

Root and rhizome data collected in 1986 after 2 years of treatment indicate that defoliation can have substantial negative impacts on belowground biomass that may limit the range of subsequent plant production in response to grazing. Both root biomass and, more importantly, N reserves in roots and rhizomes were reduced by mowing as few as 3 times during the previous growing seasons (Fig. 2). These differences in N reserves and root biomass were directly related to the aboveground production differences on intensity experiment plots in 1987. Root and rhizome nitrogen reserves are depleted during the period of rapid leaf and shoot growth early in the season (Hayes 1985). Hayes (1985) estimated that approximately half of the nitrogen in belowground structures is exported during the first half of the growing season. Reduced root biomass may also limit production by inhibiting water and nutrient uptake early in the season when growing conditions are otherwise most favorable.

Intensity vs. frequency of clipping

As suggested by Crawley (1983) and Maschinski and Whitham (1989), grazing optimization is a function of the timing of foliage removal relative to the physiological state of the vegetation. Differences between frequency and intensity experiment results support that suggestion. In this study, production was highest on frequency experiment plots that were mowed to ground level 6 times during the growing season. The most nearly comparable plots in the mowing height experiment, with respect to mowing intensity, were those plots mowed 8 times to a height of 5 cm. Mean production on the latter plots, however, was approximately 20 percent less than the maximum observed. The primary difference between the mowing regimes imposed on these sets of plots was the length of time for recovery between mowings in the first half of the growing season, when conditions for growth were most favorable. During the first half of the growing season, the mean number of days between mowings for frequency plots mowed 6 times was 25 days, while mean number of days between mowings for intensity plots mowed to 5 cm was 12 days. Thus 6x plots were allowed to recover for longer periods than were 5-cm plots. Oesterheld and McNaughton (1988) similarly reported that aboveground overcompensation for foliage removal was likely only when intervals between clipping events were extended because relative growth rates initially declined following defoliation and subsequent increases in growth rates were slow to occur.

Initial mowing dates for 6x and all height treatment plots was day 128, but initial mowing dates for 3x and 1x plots were 19 and 48 days later, respectively. Gillen and McNew (1987) reported that both maximum growth rates and maximum regrowth attained following a one-time mowing treatment declined as the time of cutting was extended into the growing season and the lower production on 3x and 1x plots is in agreement with those results.

Vegetation on intensity and frequency plots differed significantly in canopy structure. Nearly all foliage was removed at each mowing of frequency plots and typical canopy structure was allowed to reestablish. In contrast, smaller amounts were removed from 5-, 10-, and 20-cm plots at each mowing and canopies were maintained at much shorter, uniform heights. This treatment pattern created a gradient in canopy structure in which light availability to photosynthetically active tissue generally increased with amount of foliage removed. Differences in subsequent regrowth and seasonal production were then partly a function of light availability and amounts of photosynthetically active tissue. In addition, soil temperature increases resulting from soil surface exposure to solar radiation may have facilitated root uptake and microbial processes determining nutrient availability, particularly during the relatively wet late summer period in 1987 (e.g., Holland and Detling 1990).

In tallgrass prairie, aboveground production that overcompensates for foliage removal by grazers appears to be a "maximization" response mediated by grazing history. Grazing on previously ungrazed sites results in the use of reserves and root uptake capability for foliage tissue replacement. Carbon allocation to aboveground tissue is enhanced at the expense of belowground biomass. Chronic grazing, on the other hand, results in plants with fewer reserves and less capacity to supply photosynthetic demands. Overcompensation is therefore less likely. Defoliation intensity and frequency regimes superimposed on environmental conditions modify production responses within limits imposed by grazing history.

ACKNOWLEDGEMENTS

Mary Cunningham Gorman, Brenda Sweat Rongish, Sharla Bradley, Gary Wright, T. Dawn Shapley Jackson, Keith Hayward, Stacy Cloughley, Brian Jones, and Sharon Gurtz helped collect the field data. Rosemary A. Ramundo provided nutrient analyses and laboratory and coordination. This research was conducted at Konza Prairie Research Natural Area, a preserve of the Nature Conservancy operated by the Division of Biology, Kansas State University. It was supported in part by NASA Grant NAG 5-897 and NSF Long-term Ecological Research grand BSR-8514327 to Kansas State University and NSF Grant BSR-8904632 to M. I. Dyer.

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Table 1. Effects of mowing in 1985-86 on autumn, 1986, live grass root biomass (g m^{-2}), live grass rhizome N mass (g m^{-2}), and belowground N reserves (live grass root + live rhizome N mass, g m^{-2}). Treatment means represent mean values for eight replicates of each treatment. Standard errors are given in parentheses. Means with different letters were significantly different ($P < 0.05$) using Duncan's Multiple Range test.

TREATMENT	ROOTS		RHIZOME N		N RESERVES	
Unmowed	560 a	(41.6)	2.35	(0.19)	6.12	(0.46)
3x	430 ab	(36.8)	1.82	(0.21)	5.12	(0.46)
6x	379 b	(59.5)	1.76	(0.12)	4.78	(0.40)

Table 2. ANOVA results on the effects of mowing history and mowing height on cumulative grass biomass production. Separate analyses were performed for each day. Treatment means (mowing height and mowing history) represent mean values of 6 replicates. Treatment means within days with different letters indicate that treatments were significantly different using Duncan's Multiple Range test.

DAY	TREATMENT	MEAN	F VALUE	PR > F	R^2
167	Model	216.3	2.79	0.019	0.328
	Height		0.73	0.541	
	5cm	217.0			
	10cm	233.1			
	20cm	221.5			
	Control	193.8			
	History		17.22	0.0002	
	0x	256.4a			
	6x	176.3b			
	Height*History		0.12	0.947	
243	Model	457.2	4.09	0.0002	0.417
	Height		2.06	0.1211	
	5cm	461.5			
	10cm	479.2			
	20cm	485.8			
	Control	402.3			
	History		11.24	0.0018	
	0x	501.6a			
	6x	412.8b			
	Height*History		3.74	0.0186	
301	Model	446.4	5.71	0.0001	0.500
	Height		3.68	0.0198	
	5cm	449.9a			
	10cm	480.0a			
	20cm	470.1a			
	Control	385.5b			
	History		27.42	0.0001	
	0x	504.4a			
	6x	388.4b			
	Height*History		0.52	0.6720	

Table 3. ANOVA results on effects of mowing history and mowing height on N concentrations (% dry wt) in grasses. Separate analyses were performed for each day. Treatment means represent mean values for six replicates of each treatment. Means within day and source with different letters indicate that treatment means were significantly different using Duncan's Multiple Range test.

DAY	SOURCE	F-VALUE	P>F	R^2	TREATMENT	MEAN
141	Model	4.01	0.0069	0.409		1.923
	Height	4.53	0.0194		5cm	1.913ab
					10cm	1.858b
					20cm	2.004a
	History	6.59	0.0157		0x	1.974a
					6x	1.868b
	Hgt*Hist	2.19	0.1298			
154	Model	1.76	0.1542	0.246		1.646
167	Model	5.17	0.0003	0.475		1.198
	Height	11.48	0.0001		5cm	1.402a
					10cm	1.208b
					20cm	1.173b
					Control	1.008c
	History	0.0	0.951		0x	1.199
					6x	1.196
	Hgt*Hist	0.57	0.640			
175	Model	7.04	0.0002	0.540		1.456
	Height	16.57	0.0001		5cm	1.637a
					10cm	1.418b
					20cm	1.313b
	History	0.71	0.406		0x	1.476
					6x	1.436
	Hgt*Hist	0.68	0.516			
190	Model	8.64	0.0001	0.590		1.557
	Height	20.17	0.0001		5cm	1.803a
					10cm	1.537b
					20cm	1.331c
	History	0.21	0.651		0x	1.571
					6x	1.543
	Hgt*Hist	1.32	0.283			

(continued on next page)

Table 3. (continued)

DAY	SOURCE	F-VALUE	P>F	R^2	TREATMENT	MEAN
223	Model	8.34	0.0001	0.590		1.294
	Height	20.47	0.0001		5cm	1.453a
					10cm	1.309b
					20cm	1.106c
	History	0.0	0.95		0x	1.290
					6x	1.298
	Hgt*Hist	0.37	0.693			
243	Model	25.02	0.0001	0.818		0.986
	Height	57.07	0.0001		5cm	1.266a
					10cm	1.036b
					20cm	0.882c
					Control	0.782d
	History	0.20	0.660		0x	0.985
					6x	0.986
	Hgt*Hist	1.24	0.309			
301	Model	11.26	0.0001	0.669		0.656
	Height	24.68	0.0001		5cm	0.862a
					10cm	0.725b
					20cm	0.592c
					Control	0.463d
	History	1.56	0.220		0x	0.640
					6x	0.674
	Hgt*Hist	1.07	0.374			

Figure legends:

Figure 1. Aboveground production as a function of mowing frequency. Plots were mowed the same number of times in each of 3 years. Note the slight overcompensation for foliage removal in year 1 following long-term light grazing and undercompensation in years 2 and 3 after 1 and 2 years, respectively, of intense mowing. Data are from Aldous (1930).

Figure 2. Effects of defoliation on autumn grass root biomass. Error bars show 1 standard error. (A) Autumn live grass root biomass on plots clipped 6 times or left unmowed in 1985-86 and clipped to 5 cm, 10 cm, 20 cm or left unmowed in 1987. Data are plotted as percent of root biomass on plots unmowed in 1985-87. (B) Autumn grass root biomass after one year of defoliation, long-term grazing, and protection from grazing for 10 years.

Figure 3. Effect of mowing frequency on aboveground production of grasses and forbs. Error bars show 1 standard error. Means within plant type with different letters are significantly different using Duncan's Multiple Range test.

Figure 4. Effect of mowing frequency on aboveground N and P mass in grasses. Error bars show 1 standard error. Means within element with different letters are statistically different using Duncan's Multiple Range test.

Figure 5. Effect of mowing height on (A) cumulative aboveground grass production and (B) cumulative N mass in grasses at three dates in 1987. Error bars show 1 standard error. Cross-hatched bars are for plots mowed to 5cm, narrow-hatched bars for plots mowed to 10cm, wide-hatched bars for plots mowed to 20cm and

open bars for unmowed plots.

Figure 6. Effect of previous mowing frequency on grass biomass harvested to day 154. Data are plotted as a percent of harvest from plots with the same treatment in 1987 but not mowed in 1985-86. Comparisons between mowing height treatments are not valid because of inherent differences between harvest amounts. Error bars show 1 standard error.

Figure 7. Effect of current mowing height and previous mowing history on aboveground grass production in 1987. Data are plotted as a percent of production on plots not mowed in 1985-87. Error bars show 1 standard error.

Figure 8. Aboveground grass biomass dynamics on four grazed and one ungrazed tallgrass prairie sites in 1987-88. Cumulative consumption by cattle in (A) 1987 and (B) 1988. Data are plotted as percent of grass biomass produced. Aboveground grass biomass vs. day in (C) 1987 and (D) 1988. Cumulative aboveground production of grasses in (E) 1987 and (F) 1988. Solid lines and open circles indicate the ungrazed site.

Figure 1

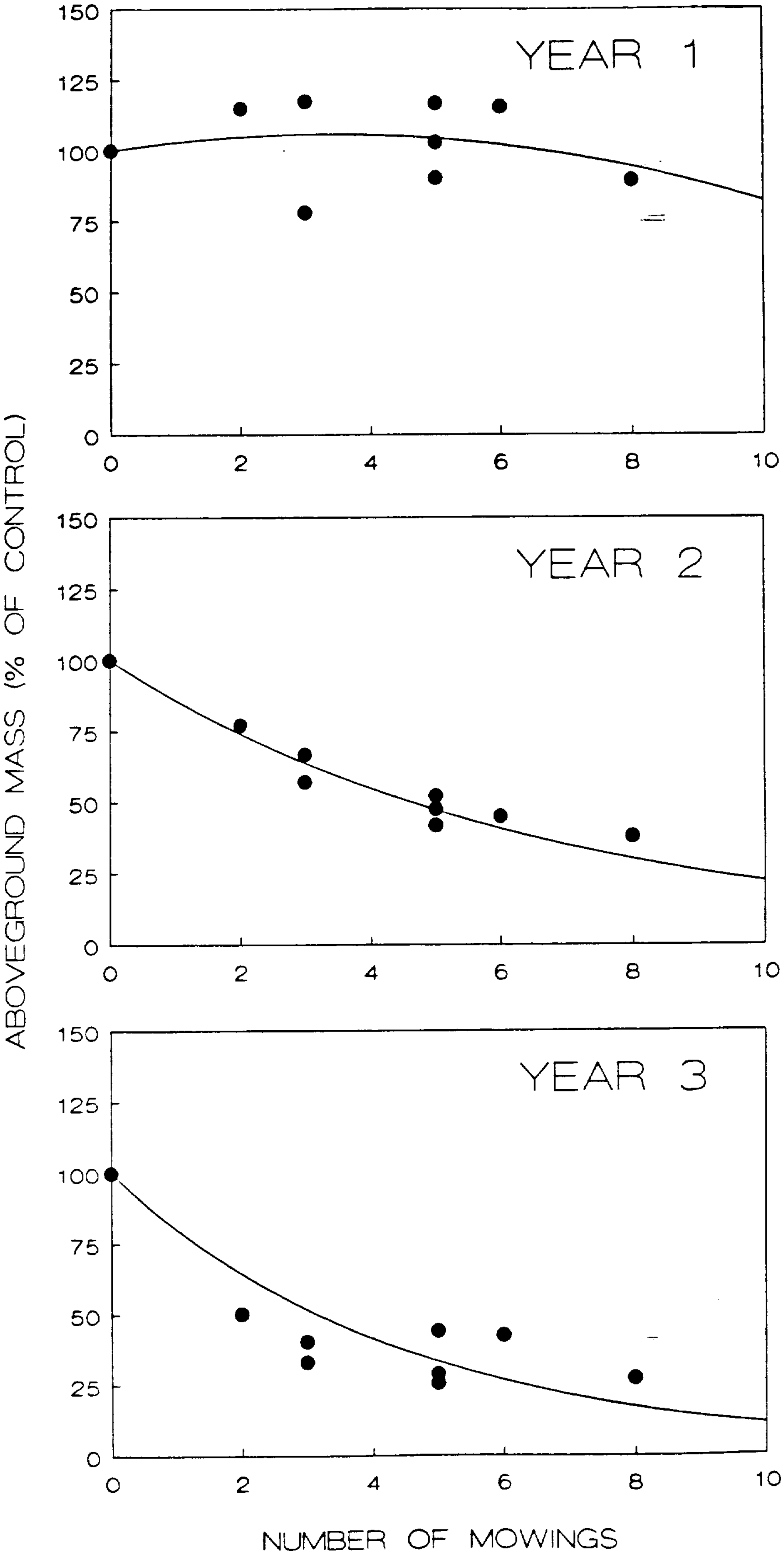

YEAR 1
YEAR 2
YEAR 3
150
125
100
75
50
25
0
0
2
4
6
8
10
ABOVEGROUND MASS (% OF CONTROL)
NUMBER OF MOWINGS

Figure 2

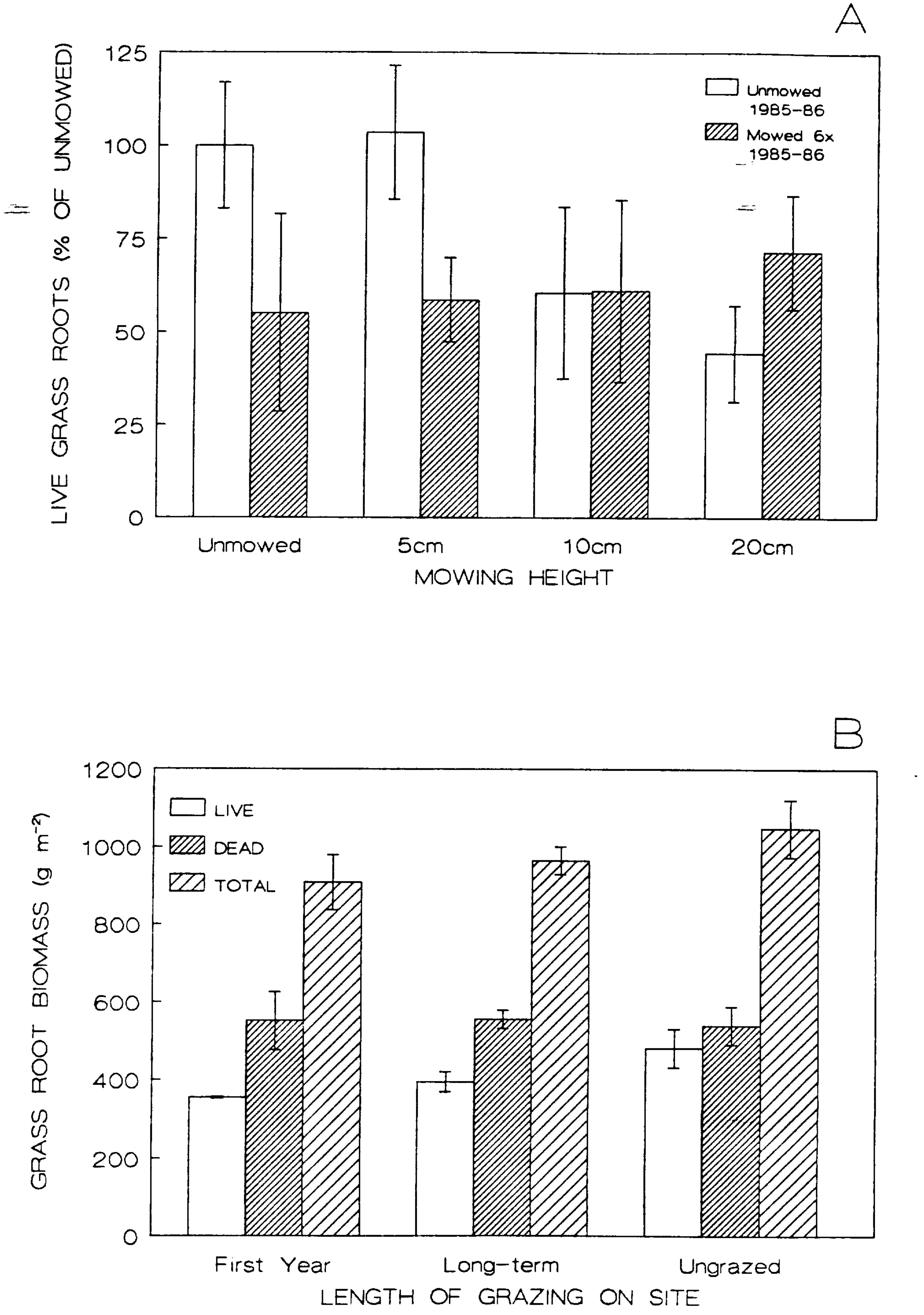
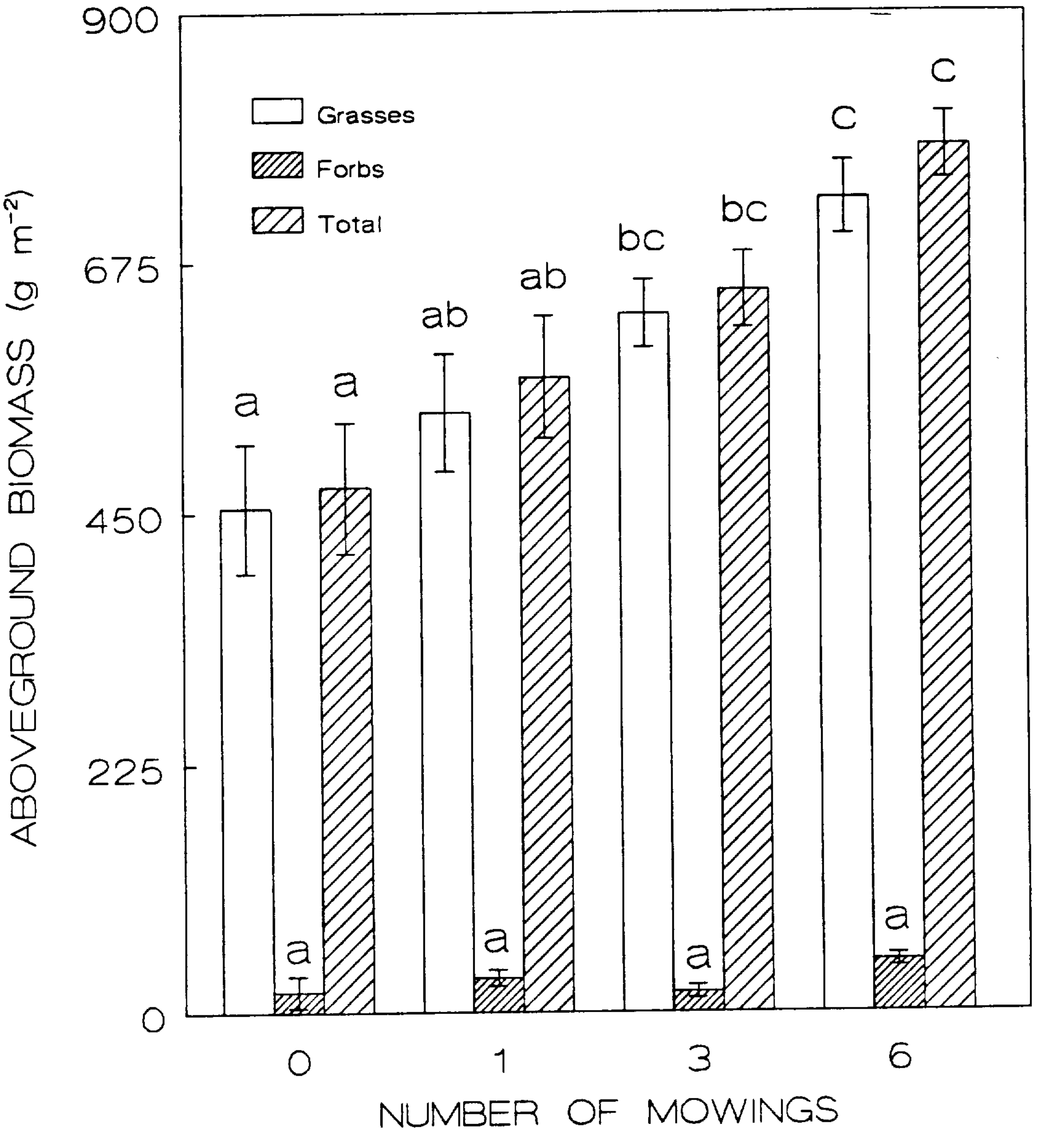
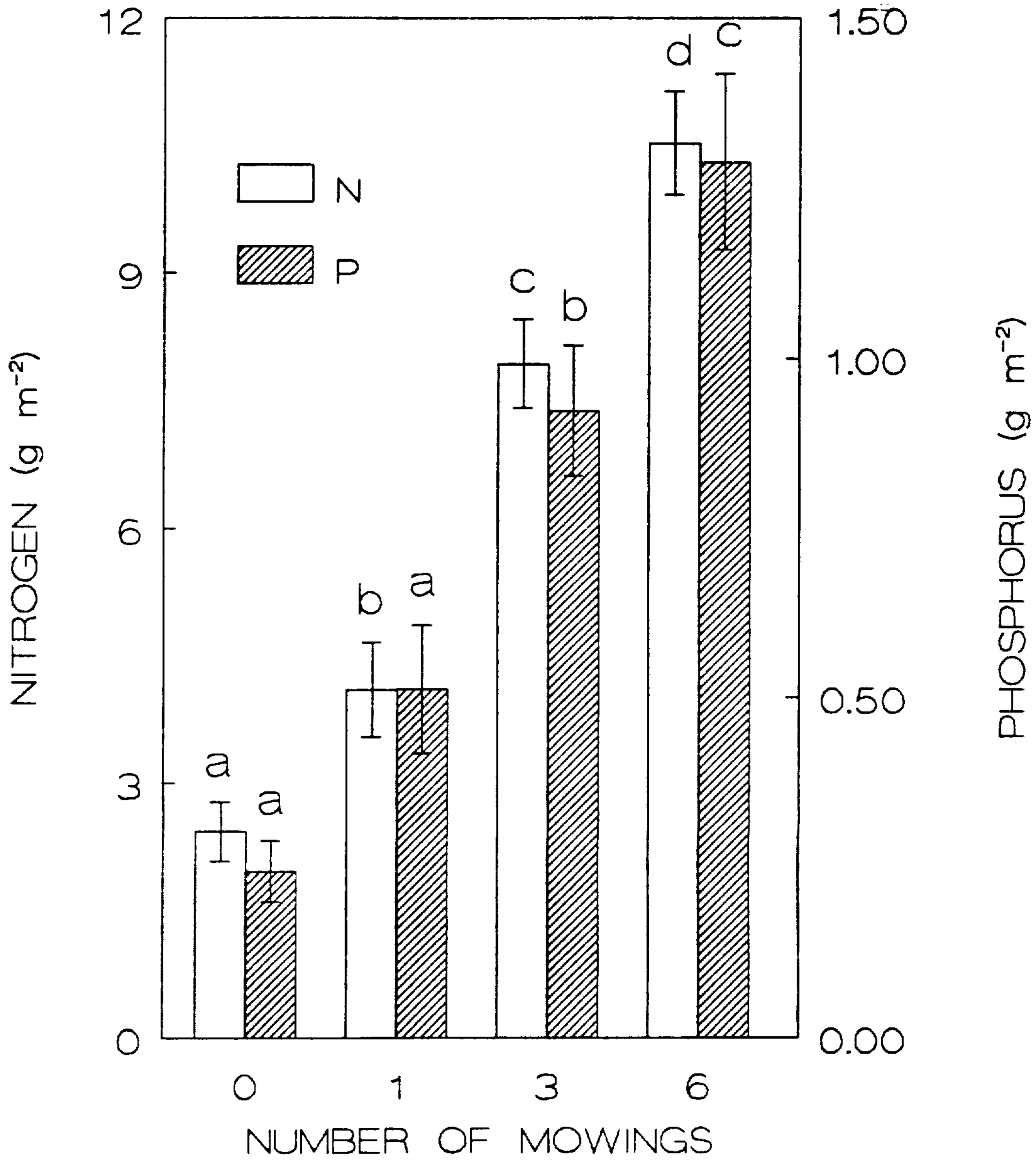

A
LIVE GRASS ROOTS (% OF UNMOWED)
125
100
75
50
25
0
Unmowed 1985-86
Mowed 6x 1985-86
Unmowed
5cm
10cm
20cm
MOWING HEIGHT
B
GRASS ROOT BIOMASS (g m^{-2})
1200
1000
800
600
400
200
0
LIVE
DEAD
TOTAL
First Year
Long-term
Ungrazed
LENGTH OF GRAZING ON SITE

Figure 3



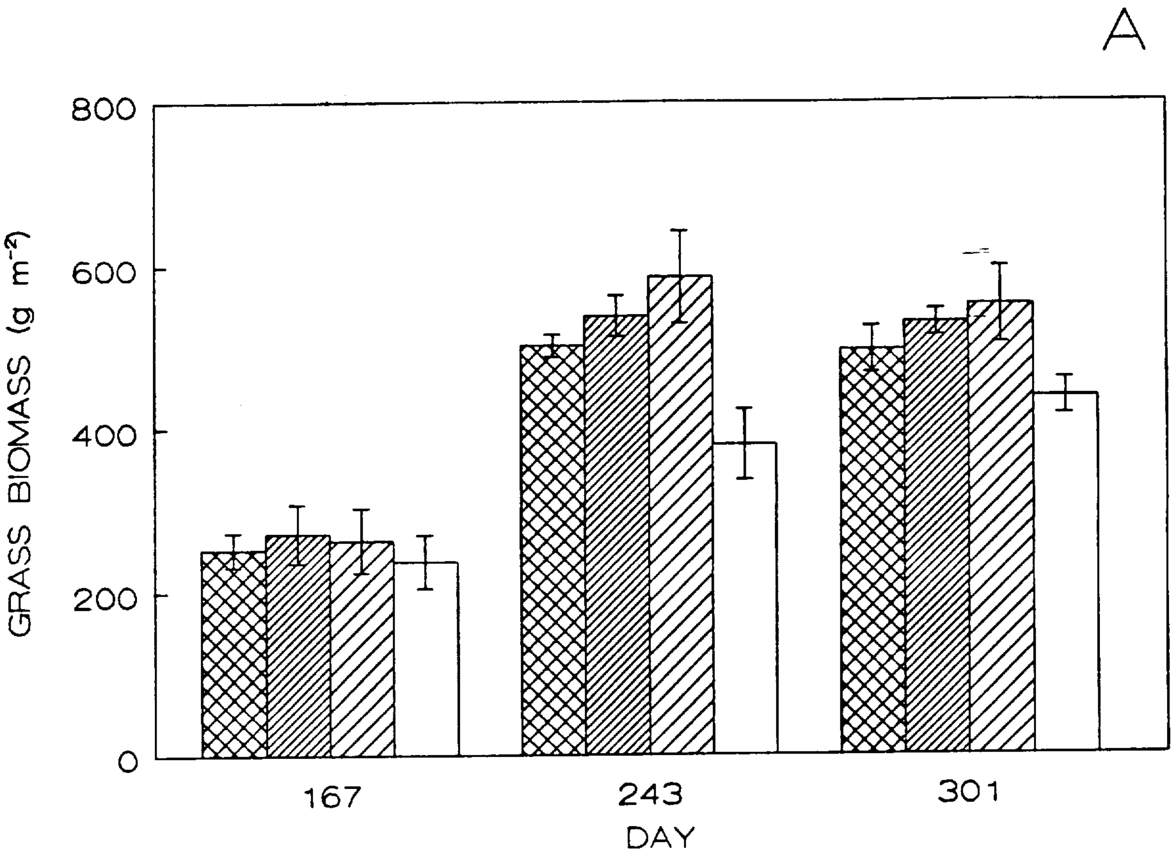
900
675
450
225
0
ABOVEGROUND BIOMASS ($g\ m^{-2}$)
Grasses
Forbs
Total
a
a
a
ab
ab
a
bc
bc
a
c
c
a
0
1
3
6
NUMBER OF MOWINGS

Figure 4



N
P
NITROGEN (g m^{-2})
PHOSPHORUS (g m^{-2})
0
3
6
9
12
0.00
0.50
1.00
1.50
0
1
3
6
NUMBER OF MOWINGS
a
a
b
a
c
b
d
c

Figure 5


A
800
600
400
200
0
GRASS BIOMASS (g m⁻²)
167
243
301
DAY

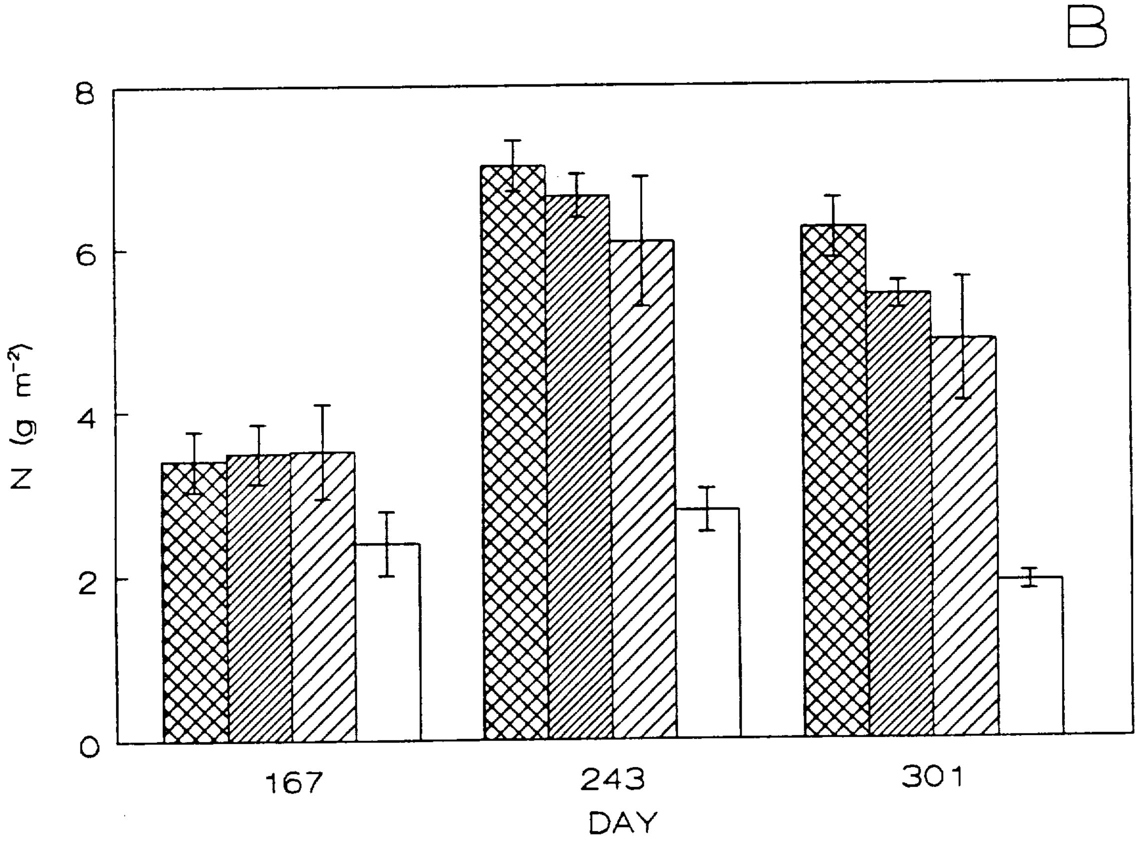

B
8
6
4
2
0
N (g m⁻²)
167
243
301
DAY

Figure 6

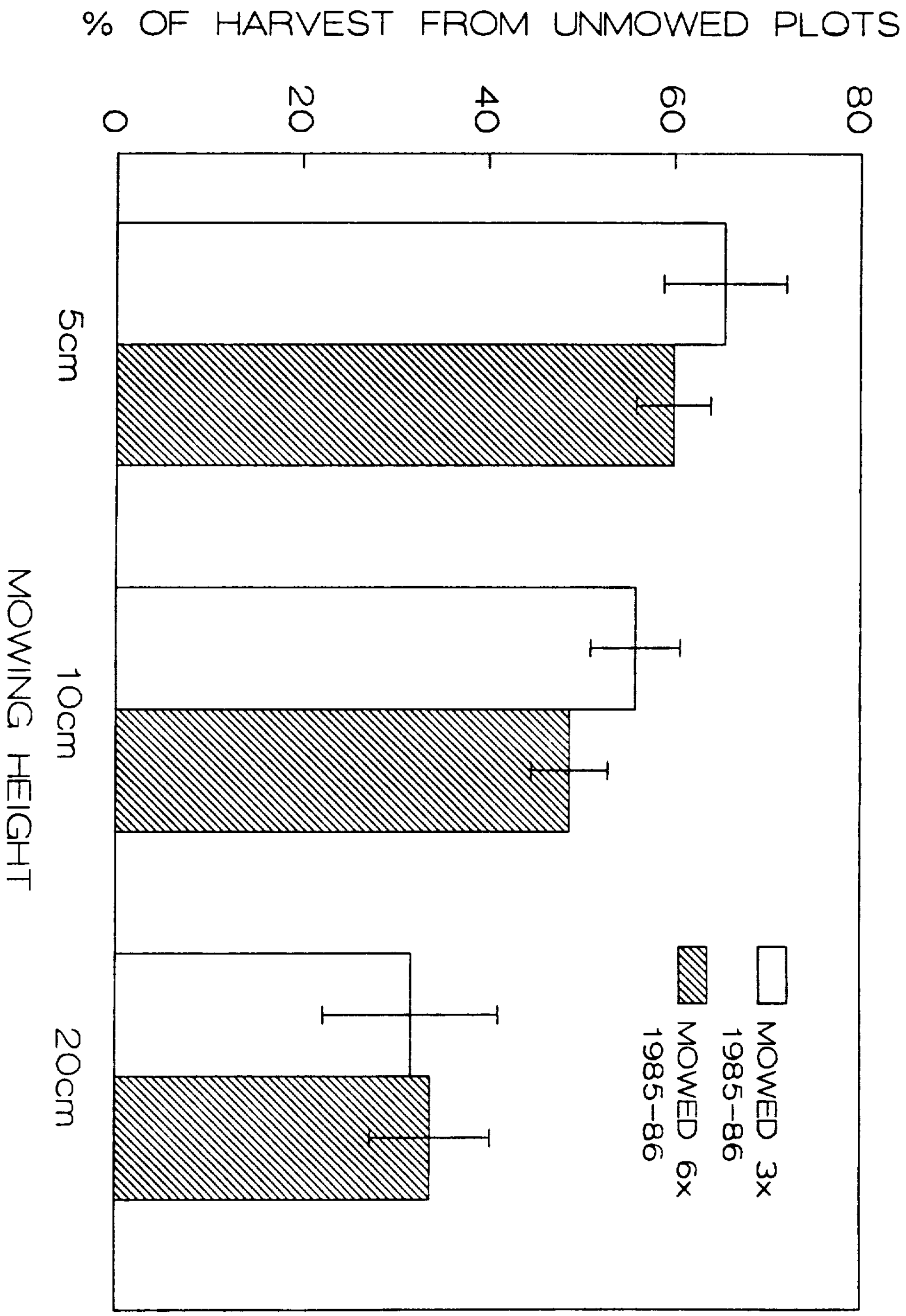

% OF HARVEST FROM UNMOWED PLOTS
0
20
40
60
80
5cm
10cm
20cm
MOWING HEIGHT
MOWED 3x 1985-86
MOWED 6x 1985-86

Figure 7

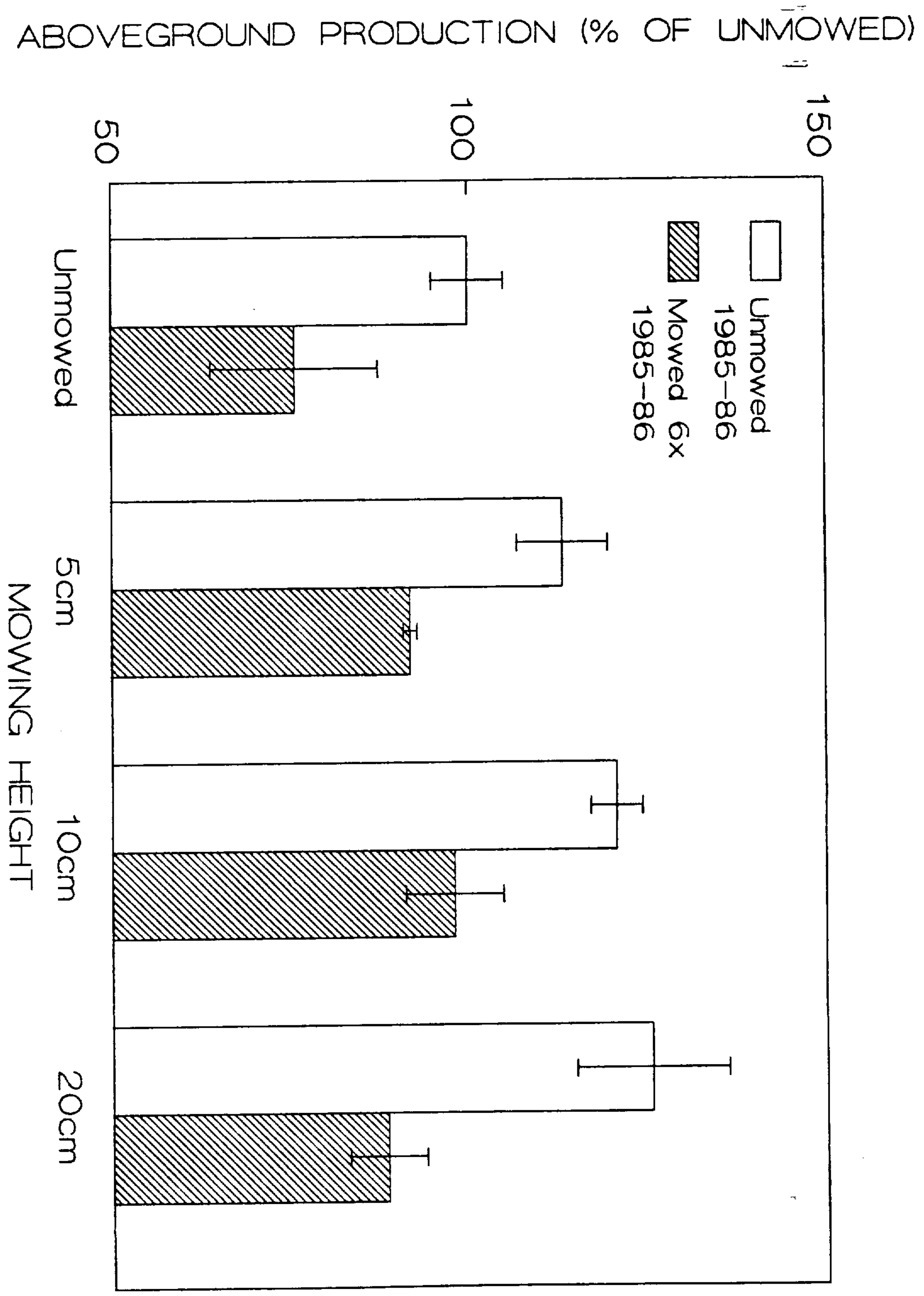
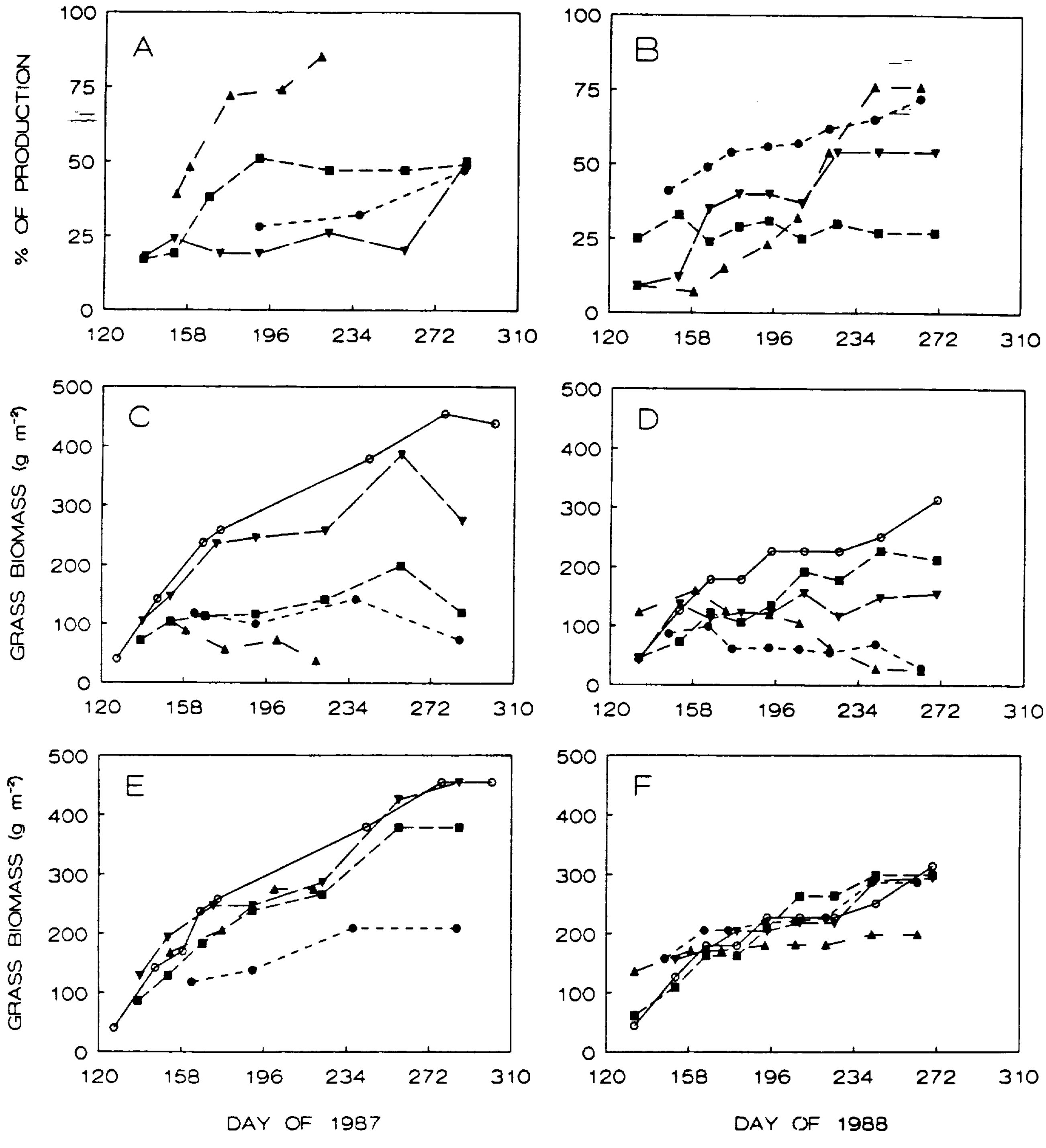

ABOVEGROUND PRODUCTION (% OF UNMOWED)
50
100
150
Unmowed 1985-86
Mowed 6x 1985-86
Unmowed
5cm
10cm
20cm
MOWING HEIGHT

Figure 8


A
B
C
D
E
F
% OF PRODUCTION
GRASS BIOMASS (g m⁻²)
GRASS BIOMASS (g m⁻²)
0
25
50
75
100
0
100
200
300
400
500
120
158
196
234
272
310
DAY OF 1987
DAY OF 1988

GROWTH AND TRANSITION: REMOTE SENSING AND GEOGRAPHIC INFORMATION SYSTEMS AT KANSAS STATE UNIVERSITY

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ABSTRACT: Remote sensing and geographic information systems education and research at Kansas State University have grown tremendously in the past decade. Dramatic improvements in hardware and software have enhanced offerings in a wide range of spatial analysis (including remote sensing) courses. Success in extramural funding through such agencies as the U.S. Agency for International Development and the National Science Foundation, have created a major research thrust in Kansas State University's Geography and Biology programs relative to the application of remote sensing and geographic information systems for natural resource assessment and landscape ecology. The State of Kansas initiatives have also enhanced Kansas State University's role in providing a significant contribution in remote sensing/geographic information systems research and education.

INTRODUCTION

Since the first remote sensing of the environment course taught in 1976 in the geography program at Kansas State University (KSU), remote sensing (and new developments in geographic information systems) teaching and research have expanded dramatically. Beyond the education component, the primary research thrusts at KSU are in two particular areas: remote sensing and geographic information system approaches to natural resources assessment; and, remote sensing and geographic information system approaches to landscape ecology. Current developments associated with the establishment of a Geographic Information System/Spatial Analysis Laboratory (GISSAL) and networked facilities with the KONZA Long Term Ecological Research remote sensing/GIS data management center have created a dynamic remote sensing initiative.

REMOTE SENSING EDUCATION AT KANSAS STATE UNIVERSITY

The first remote sensing course was taught at Kansas State University in 1976. Before this time aerial photographic interpretation and terrain analysis were taught as part of courses in the Department of Geography and Civil Engineering.

Since 1976, remote sensing and related offerings at Kansas State University have increased dramatically. There are currently 11 courses in two departments (with emphasis in the geography department) at both the undergraduate and graduate level. As software and hardware facilities have increased, the complexity and integration of spatial approaches associated with remote sensing at Kansas State University has also been increased. For example, courses in geographic information systems support innovative integration of coverage layers in remote sensing analyses.

Research and instructional software resources at KSU are largely interchangeable. ERDAS, RSVGA, and MSIMAGER are PC packages used for analysis of SPOT and LANDSAT imagery, as well as for some GIS functions. Both ARCINFO and PC-ARCINFO workstations are used at KSU for GIS applications, supplemented by IDRISI on a PC. Coverages developed with ERDAS can be imported as layers in ARCINFO and IDRISI. The speed and flexibility of CAD packages on a 386 or 486 PC make them preferable for editing of information layers to be imported into ARCINFO. In particular, Evolution Computing's EASYCAD and FASTCAD, both written in Assembly language, are heavily used at KSU for the editing of DXF files which are easily imported into the ARCINFO environment. Maps for internal review and final project papers at KSU are produced by a variety of packages on a PC. Choropleth maps are generated from ATLAS-PRO, MAP-INFO (in both DOS and WINDOWS versions), and MAP-VIEWER, a WINDOWS package which also outputs graduated-symbol and 3-D prism maps. SURFER is used to produce contour and 3-D fishnet plots. CAD packages are utilized when it is necessary to produce qualitative-symbol maps. Database work centers on the use of dBASE IV and FOX-PRO. Scanning and editing at KSU is based on Scorpion Technology's SRV-386 which runs as an addition to AUTOCAD version eleven and controls an E-size scanner.

GISSAL was created in August, 1990, as an outgrowth of the Department of Geography's continued expansion in hardware and software capabilities in support of remote sensing, geographic information systems, and computer mapping. Current GISSAL projects are funded by the U.S. Agency for International Development, U.S. Soil Conservation Service, National Science Foundation, Kansas GIS Policy Board/Kansas Water Office, Kansas Wildlife and Parks, National Aeronautics and Space Administration, and the Kansas State University Agricultural Experiment Station. GISSAL also cooperates closely with Konza Prairie Long-Term Ecological Research Site's remote sensing/geographic information system laboratory on various other projects.

REMOTE SENSING RESEARCH AT KANSAS STATE UNIVERSITY

KSU has had a series of major research efforts relating remote sensing and geographic information systems to natural resource analysis. Nellis (with Lulla and Jensen, 1990) has provided an overview of the interface of geographic information systems and remote sensing for rural land use and natural resource analysis. The identified thrusts in this review have been a particular focus at

Kansas State University (Nellis 1988).

The use of remote sensing and geographic information systems for water resource analysis is one of the natural resource research areas at KSU. Landsat multispectral and thematic mapper data, for example, have been used to predict water demand in irrigated areas of western Kansas (Nellis, 1986 and 1987). The approach involved combining remote sensing data with weather data and irrigation methods to estimate groundwater use from the Ogallala Aquifer. Results are being used by water resource planners in groundwater management districts to more fully address planning objectives as outlined in the Kansas Water Plan.

Through a National Conservation Strategy, the government of Botswana is attempting to implement a philosophy focusing on humanity's relationship with the biosphere, and the need for sustainable development of natural resources. KSU researchers are combining with other researchers to provide baseline spatial information in support of Botswana's National Conservation Strategy. Nellis and Bussing (1989, 1990), for example, have used SPOT HRV multispectral data, and Landsat thematic mapper and multispectral data for analyzing the spatial variation in elephant impact in the Chobe National Park, Botswana, and in analyzing the extent of desertification due to overgrazing in areas fringing the Makgadikgadi Pans of central Botswana. Nellis, et al., (1990) have also used video digitized Space Shuttle Photography to study generalized patterns of wildlife impact in the Chobe District. In a broader context, the use of remote sensing and geographic information systems for natural resource management at the Botswana district level (regional) have also been initiated (Bussing, et al., 1989).

Another major remote sensing research thrust at KSU focuses on understanding the landscape ecology of the tallgrass prairie ecosystem, particularly the Konza Prairie Research Natural Area. The Konza Prairie (an area of approximately 3500 hectares), is located in the Flint Hills region about 10 km south of Manhattan, Kansas. The area is owned by Nature Conservancy and leased to KSU. The area is one of 17 sites funded through the National Science Foundation for long-term ecological research. The area is dominated by big bluestem (Andropogen gerardii), little bluestem (A. scoparius), Indiangrass (Sorgastrum nutans) and switchgrass (Planicum virgatum). Research has focused on the role of fire and grazing systems. Studies have varied in complexity from direct mapping of burned versus unburned watersheds using video digitized areal photography (Nellis, 1986) and satellite data sets (Nellis and Briggs, 1987) to more complex analysis of landscape heterogeneity using textural algorithms applied to SPOT HRV data (Briggs and Nellis, 1991).

In addition, general pattern recognition using SPOT HRV multispectral data of the Konza Prairie were analyzed by Nellis and Briggs (1988). Briggs and Nellis (1989) used Landsat thematic mapper data of selected Konza watersheds to predict above-ground prairie biomass and investigated the effect of spatial scale on Konza landscape classification (Nellis and Briggs, 1989). Further, the integration of SPOT satellite data and digital elevation models (DEM) data allowed for second-order soil surveys of the Konza Prairie (Su et al., 1990).

The Konza Prairie Research Natural area and surroundings have also been the site of the First International Satellite Land Surface Climatology Project (ISLSCP) Field Experiment (FIFE), an international, land-surface-climatological experiment. The objectives of FIFE are to better understand the role of biology in controlling the interactions between the atmosphere and the "vegetated" land surface, and to investigate the use of satellite observations to infer climatologically significant land surface parameters (Sellers et al., 1988). As a result of FIFE, KSU researchers have generated a wealth of remote sensing data, and research results, furthering understanding of the Konza prairie and its surrounding ecosystems (such as Dyer, et al. 1991).

At near ground level (using a Barnes Modular Multiband radiometer and an Exotech Model 100-A Radiometer), Kansas State researchers Weiser et al., (1986) have provided insights on the use of spectral measurements of Konza Prairie in estimating grass canopy leaf area index (LAI) and total aboveground green phytomass. Using similar remote sensing techniques, Asrar, et al., (1989) evaluated diurnal and seasonal spectral reflectance characteristics on Konza Prairie burned and unburned watersheds, based on field measurements and models of radiation transport in plant canopies.

Kansas State researchers have also provided approaches for understanding radiant energy distribution in leaf canopies of agricultural crops, such as soybeans, maize, and sugarbeets. Myneni et al., (1988), for example, used a finite element discrete ordinates method for solving the radioactive transfer equation in non-rotationally invariant scattering media, and its application to the leaf canopy problem. Myneni and Kanemasu (1988), also documented the possibility of detecting the hot spot (peak in reflected radiation in the retro-solar direction) of vegetation canopies using a conventional radiometer.

NEW INITIATIVES: KANSAS GIS POLICY BOARD AND KSU.

As a result of Kansas Legislative funding and Governor approval, the Kansas Geographic Information System Policy Board was created in 1989. The Board is charged with overall coordination for implementing and using geographic information system technology by Kansas Agencies. The Board includes twenty-one members representing Kansas agencies, universities, local units of government, and associated federal government units.

Four parallel tracks have been developed by the Kansas GIS Policy Board to address the strategic plan: database development, technology transfer, service development, and overall management. One component of the database track is a Kansas soil resources computer formatted database. Since November

1990, the Departments of Geography and Agronomy at KSU have been scanning and editing Kansas county soil surveys. The derived GIS information will be used with other spatial data for a wide range of natural resource/geographic information systems planning initiatives (Nellis, 1991).

CONCLUSIONS

Remote sensing and geographic information systems education and research has undergone a tremendous transformation at Kansas state University in the past decade. The establishment of the Geographic Information Systems/Spatial Analysis Laboratory (GISSAL) as well as success in competing for extramural grants has led to major remote sensing GIS research initiatives in the area of landscape ecology and natural resource assessment. The continued enhancement (through improvements in hardware, software, and degree of network integration) of the geography and biology programs at Kansas State University provides a foundation for an exciting research agenda in the future.

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Transformed Vegetation Index for Measuring Spatial Variation in Drought Impacted Biomass on Konza Prairie, Kansas

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ABSTRACT

Landsat thematic mapper satellite data were found to offer potential for regular monitoring of the Konza Prairie tallgrass prairie ecosystem. Data from two Landsat thematic mapper channels derived from an August 1989 scene were analyzed using a transformed vegetation index relative to above ground biomass samples on burned and unburned watersheds for Florence and Clime soils. In addition transformed vegetation index (TV1) values were analyzed relative to watersheds experiencing different burning frequency. Despite drought conditions during 1989, the combination of using Landsat thematic mapper in a transformed vegetation index provided a suitable measure of spatial variation in above ground biomass for diverse burning strategies and soil conditions.

Traditional techniques for estimating the productivity of grasslands under varying treatments and soil conditions are time consuming, costly, and do not lend themselves to evaluation of geographically large areas. Vegetation indices, derived using satellite data, however, offer the potential for extrapolating limited ground samples to watershed units.

Since the early success of the Landsat system in the early 1970's, scientists from throughout the world have explored the question of measuring vegetation dynamics with remote sensing digital data. In 1982 and 1984, N.A.S.A. launched the Landsat thematic mapper sensor on the Landsat satellite which offered improved spatial resolution with additional improvements in the spectral band resolutions from the Landsat multispectral scanner. The objective of this paper is to explore the use of Landsat thematic mapper data for understanding the condition of various watersheds on the Konza Prairie

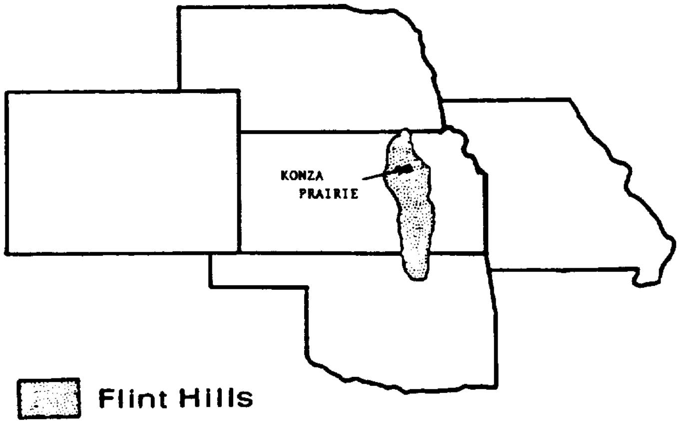

Fig. 1. Konza Prairie, located just south of Manhattan, within the Flint Hills of Kansas.

Research Natural Area, Kansas experiencing different burning treatments under varying soil conditions. The particular year of the Landsat thematic mapper data is 1989; a year of drought, which contrasts with other remote sensing studies of Konza under near normal precipitation conditions.

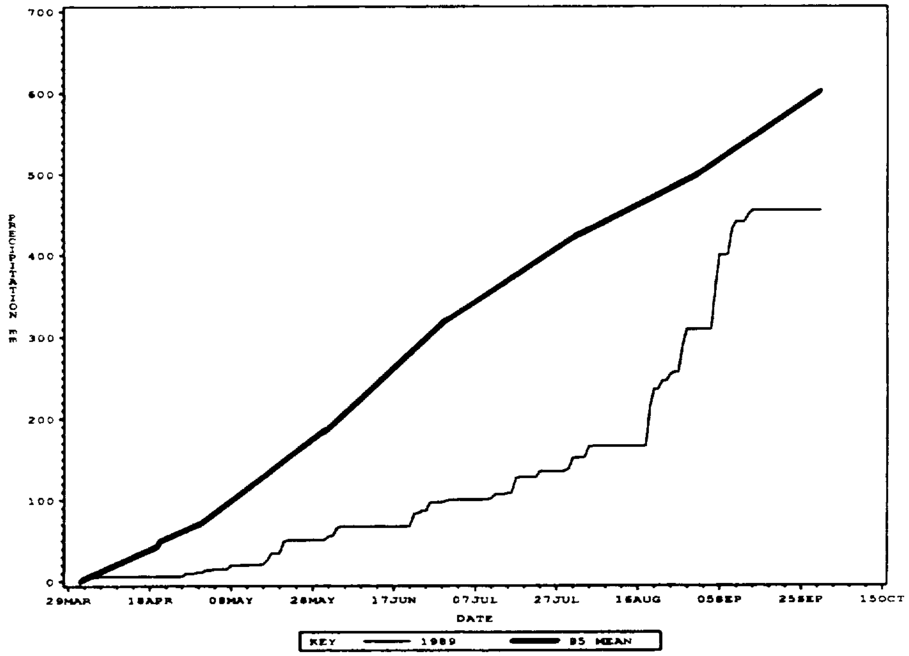

Fig. 2. Precipitation for the 1989 growing season relative to the 95-year mean.

Fig. 3. Transformed Vegetation Index (TVI) image of the Konza Prairie, lighter tones represent higher (TVI) values.

STUDY AREA

The Konza Prairie Research Natural Area is a tallgrass prairie ecosystem located in the Flint Hills region about 10 km south of Manhattan, Kansas (Fig. 1). This 3487-ha area is largely native grassland dominated by big bluestem (*Andropogon gerardii*), little bluestem (*A. scoparius*), Indiangrass (*Sorgastrum nutans*), and switchgrass (*Panicum virgatum*). The reserve is owned by Nature Conservancy and leased to Kansas State University for long term ecological research. Konza Prairie is representative of the Flint Hills Upland, a band of rolling hills roughly 70 km wide, and extending across Kansas north–south from Nebraska to Oklahoma. The hills are characteristically steep-sided with distinctive benches above limestone members. Local relief on Konza is approximately 124 meters, although local relief of approximately 60 meters is more common (Briggs and Nellis, 1991).

Soils on slopes and uplands are typically shallow and rocky, while valleys have deep, permeable soils. The two soils represented in this study are the Florence and the Clime series. The Florence series consists of moderately deep, sloping and moderately steep soils on uplands. These soils are underlain by limestone bedrock and formed in residuum weathered from cherty limestone. The Florence soils are well drained. In contrast, the Clime series consists of moderately deep, sloping to moderately steep, calcareous soils on uplands. These soils formed in residuum weathered from calcareous clayey shale. Clime soils are moderately well drained to well drained (Jantz et al., 1975).

Under an experimental plan initiated in 1971, different watershed units were placed under a variety of prescribed burning (generally in early to mid-April) regimes ranging from annual to 2, 4, 10, and 20 year intervals (Marzolf, 1988).

MATERIALS AND METHODS

A 4 August 1989 Landsat thematic mapper digital data set was the primary data input for the study. The August 1989 scene was selected to analyze the potential application of the Landsat thematic mapper sensor under significant drought conditions for the Konza tallgrass prairie ecosystem. August was the month of maximum drought impact prior to some late season precipitation (Fig. 2).

The Landsat thematic mapper provides repetitive coverage of a given location on the earth every 16 days. The Landsat thematic mapper has seven bands: Band 1 (0.45–0.52 micrometers, blue-green); Band 2 (0.52–0.60 micrometers, green); Band 3 (0.63–0.69 micrometers, red); Band 4 (0.76–0.90 micrometers, near infrared); Band 5 (1.55–1.75 micrometers, mid-infrared); Band 6 (10.4–12.5 micrometers, far infrared); and Band 7 (2.08–2.35 micrometers, mid-infrared). The spatial resolution of the thematic mapper is 30 by 30 meters, with each pixel (30 by 30 meter area) represented by a brightness value per band that may vary from 0–255 (Campbell, 1987).

Vegetation indices are quantitative measures, based upon digital input values, that attempt to measure biomass or vegetative vigor. Usually a vegetation index is formed from combinations of several spectral values that are added, divided, or multiplied in a manner designed to yield a single value that indicates the amount or vigor of vegetation within a pixel or pixel matrix. For this study a transformed vegetation index (TVI) was applied to the data set using the equation,

$$\mathrm{TVI} = \left[\frac{\mathrm{DN\ Band\ 4} - \mathrm{DN\ Band\ 3}}{\mathrm{DN\ Band\ 4} + \mathrm{DN\ Band\ 3}} + 0.5\right]^{1/2} \times 100$$

where, the DN represents the digital value for bands 4 and 3 of the Landsat thematic mapper system (Lillesand and Kiefer, 1987). In past studies, ground reference data collected and compared to the TVI of the same area, have been found to covary with the green biomass present for the pixel value represented by the TVI (Campbell, 1987).

In this study the resulting TVI values by watershed and sub-watershed (based on soil series distribution) were analyzed relative to actual live above ground biomass (for selected sample clipped areas), burning frequency, and underlying soil condition. Figure 3 represents a transformed vegetation index

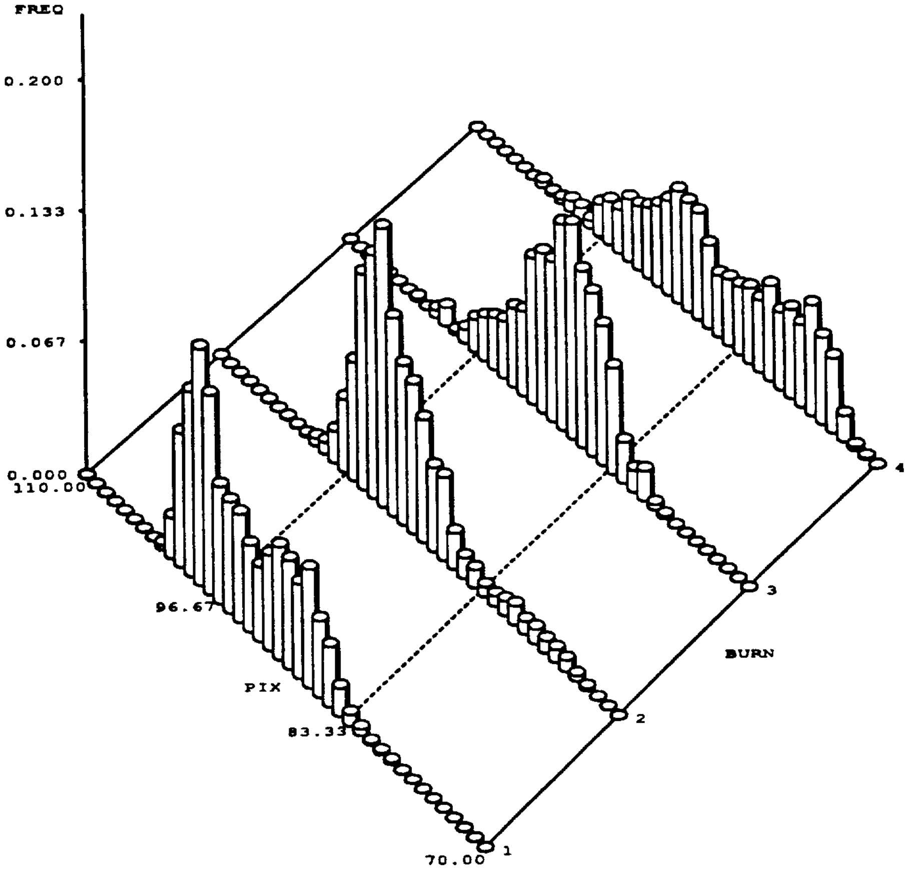

Fig. 4. Transformed Vegetation Index frequency on various soil types for variable burning frequencies.

of the Konza Prairie. This particular research focuses on watersheds not impacted by grazing activities.

RESULTS

The results of this study demonstrate the ability to characterize watersheds and sub-watersheds based on burning frequency and soil conditions. When contrasting the transformed vegetation index for watersheds burned more frequently versus less frequently on the Florence relative to the Clime soil series, the moderately deep Florence soils generate a higher greenness index, with those burned at a greater than 4 year interval producing the highest level value of TVI (Fig. 4). The degree of variation in the less frequently burned Florence watershed, however, had a higher degree of variation in

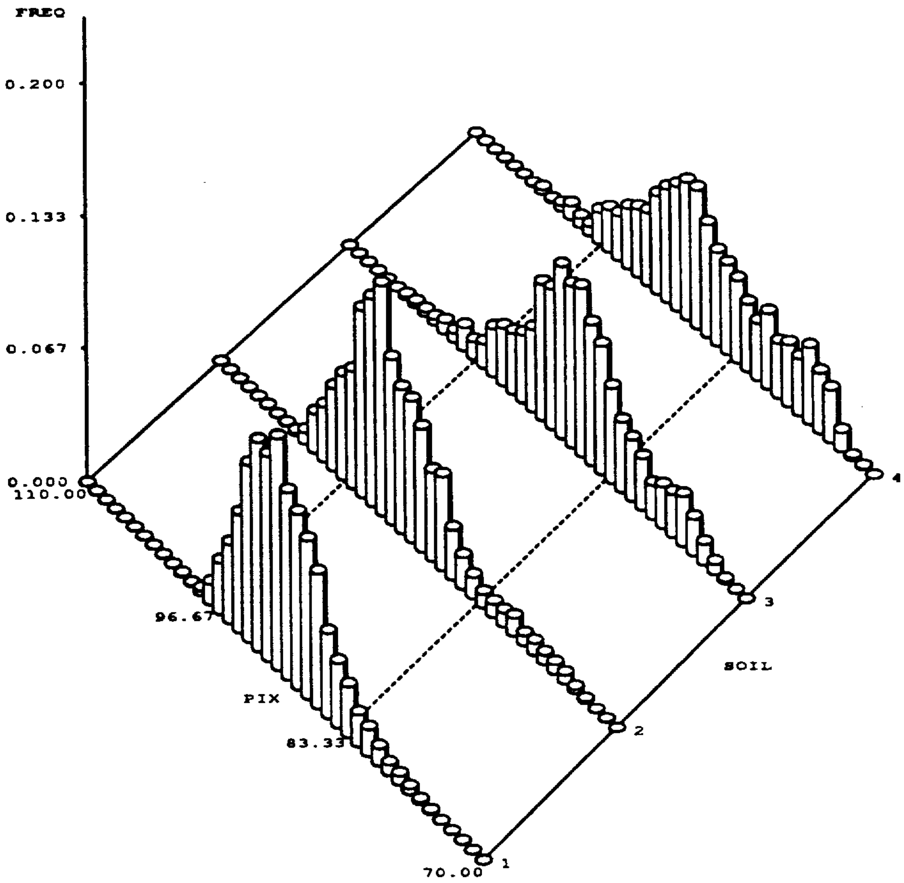

Fig. 5. Transformed Vegetation Index frequency on burned and unburned Florence and Clime soil series.

the TVI values generated. Thus, those watersheds burned more frequently, had a more clustered, and therefore more uniform TVI value, despite the slightly lesser vegetative vigor resulting from a greater drought impact. This same spatial pattern exists for the watersheds treated under the Clime soil series, although the degree of TVI variability is just the opposite of the Florence soils watersheds. This may be the result of the Clime soil's higher clay component and less well drained characteristic which may lead to greater TVI variability on the more frequently burned watersheds.

In comparing the TVI values by soil series for burned and unburned watersheds, the burned watersheds were only slightly higher in TVI values than unburned watersheds (Fig. 5). The degree of variability, however, is greatest for the Florence versus the Clime soil series. This may be caused by the textural contrast between the Florence and Clime soils, degree of soil depth, and parent material variations.

CONCLUSIONS

The utility of the transformed vegetation index, with input of Landsat thematic mapper data, in understanding larger scale watershed response to drought under various soil conditions and burning treatments proved to be useful. In particular, vegetative vigor variability for watersheds with different burning frequencies were effectively described using Landsat thematic mapper data.

Future research is needed to contrast transformed vegetation index values for non-drought conditions, and for coupling the transformed vegetation index with other spatial data sets such as slope aspect. The need for remote sensing in combination with other spatial data sets will play an increasingly important role in understanding large scale dynamic changes in the tallgrass prairie ecosystem.

ACKNOWLEDGMENTS

This research was funded by NSF grant BSR-9011662 for Long-Term Ecological Research at Kansas State University.

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APPENDIX E

Controls of nitrogen limitation in tallgrass prairie

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Received August 22, 1990 / Accepted in revised form January 7, 1991

Summary. The relationship between fire frequency and N limitation to foliage production in tallgrass prairie was studied with a series of fire and N addition experiments. Results indicated that fire history affected the magnitude of the vegetation response to fire and to N additions. Sites not burned for over 15 years averaged only a 9% increase in foliage biomass in response to N enrichment. In contrast, foliage production increased an average of 68% in response to N additions on annually burned sites, while infrequently burned sites, burned in the year of the study, averaged a 45% increase. These findings are consistent with reports indicating that reduced plant growth on unburned prairie is due to shading and lower soil temperatures, while foliage production on frequently burned areas is constrained by N availability. Infrequent burning of unfertilized prairie therefore results in a maximum production response in the year of burning relative to either annually burned or long-term unburned sites.

Foliage biomass of tallgrass prairie is dominated by C_4 grasses; however, forb species exhibited stronger production responses to nitrogen additions than did the grasses. After four years of annual N additions, forb biomass exceeded that of grass biomass on unburned plots, and grasses exhibited a negative response to fertilizer, probably due to competition from the forbs. The dominant C_4 grasses may out-compete forbs under frequent fire conditions not only because they are better adapted to direct effects of burning, but because they can grow better under low available N regimes created by frequent fire.

Key words: *Andropogon gerardii* – Fire – Nitrogen – Prairie – Productivity

Community nutrient limitation, as measured by the extent to which primary production is enhanced when nutrient limitations are removed, is controlled by 1) different nutrient immobilization potentials of soils, 2) differences in soil fertility, and 3) differences in nutrient demands associated with plant physiological status (Chapin et al. 1986). Fire in tallgrass prairie has the ability to influence plant physiological status and growth efficiencies (Knapp 1985), plant nitrogen use efficiencies (Ojima 1987), and soil nutrient availability (Eisele et al. 1989, Ojima et al. 1990, Seastedt and Ramundo 1990) while having relatively small effects on plant species composition (Gibson and Hulbert 1987; Gibson 1988). Thus, we hypothesized that community nutrient limitation in grasslands would vary depending upon the fire history of an area, even though species composition across these areas would remain similar.

The frequency of disturbances such as fire may impose unique characteristics on the system (Trudgill 1977; Huston 1979; Reiners 1983; Gibson 1988). Hulbert and Wilson (1983) reported that infrequently burned sites (sites burned at 2 or 6 year intervals) tended to have higher foliage biomass the year that they were burned than did annually burned sites. Ojima (1987) modified the CENTURY model of Parton (e.g. Parton et al. 1987) to study

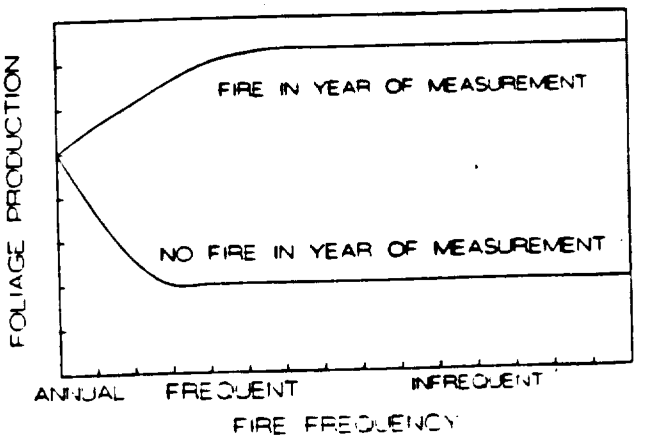

Fig. 1. Hypothesized foliage response to fire frequency, given that sites are burned in year of measurement or not burned in year of measurement

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the effects of fire on prairie productivity and N dynamics. The model predicted a greater productivity response to fire on infrequently burned sites in the year of burning compared to either annually burned or long-term unburned sites that remain unburned (Fig. 1). This result occurred because N availability to plants was controlled by 1) total soil N input-output relationships, which are negatively affected by frequent burning and 2) by the C:N ratio of the soil organic matter. In the model, fire stimulated root growth and root death, which in turn increased C inputs to soil. This fixed C was exploited by microbes, which immobilized available soil N in the year following fire; less N was therefore available to plants. Hence, annually burned sites should be chronically N-limited. Foliage production of tallgrass prairie usually decreases under unburned conditions due to self-shading and temperature limitations created by the build-up of detritus; hence, the microbial immobilization potential for available soil N is not maintained on unburned prairie.

Field data on plant and soil N dynamics support many of CENTURY's predictions (Ojima 1987; Ojima et al. 1990; Seastedt 1988; Seastedt and Hayes 1988; Hayes and Seastedt 1989; Wedin and Tilman 1991), but direct tests of the model are few. Hulbert (1988), for example, had found that plots clipped in early spring to remove litter and standing dead vegetation showed a 39% increase in foliage biomass in response to N additions, while unclipped plots (with litter) increased only 11%. Old (1969) reported an opposite effect; fertilized plots burned in the year of measurement produced only 5% more biomass than controls while unburned, fertilized plots (burned 3 years earlier) produced 43% more foliage than unfertilized plots.

We tested this hypothesized relationship between N limitation and fire frequency with a series of fertilization experiments. If our conceptual model and the CENTURY predictions are correct, then 1) unburned prairie should have relatively low N demands and so be relatively unresponsive to fertilizer additions, 2) annually burned sites should experience intense N limitation and so be highly responsive to fertilizer additions, 3) following fire, infrequently burned prairie should be less responsive to fertilizer additions than should annually burned prairie, but given the superior temperature and light regime of these sites, their response to N will be greater than that of unburned sites, and 4) given the removal of both energy and N restrictions, infrequently burned prairie should exhibit the largest production response of all unfertilized treatments.

Study site and methods

Research was done on the Konza Prairie Research Natural Area, a long-term ecological research (LTER) site owned by The Nature Conservancy and managed by Kansas State University. The area is on the western edge of the tallgrass prairie biome in the Flint Hills of northeastern Kansas. Konza Prairie consists of watersheds burned in late spring every 1, 2, 4, 10, or 20 years. This fire management program has been operating on portions of the site since 1970. Reports are available describing the flora of the site (c.f. Gibson 1988), plant productivity (Abrams et al. 1986; Briggs et al. 1989) and N dynamics (Ojima 1987; Ojima et al. 1990; Seastedt 1988; Seastedt and Hayes 1988; Hayes and Seastedt 1989). The dominant plant species include big bluestem (*Andropogon gerardii* Vit.), little bluestem (*A. scoparius* Michx.), and Indiangrass [*Sorgastrum nutans* (L.) Nash]. Among the common forbs (non-grass, non-woody vascular plants) are goldenrods (*Solidago* spp.), milkweeds (*Asclepias* spp.), leadplant (*Amorpha canescens* Pursh), ironweed (*Vernonia baldwinii* Torr.), and numerous other asters. While portions of the site have been grazed by cattle or bison, only data obtained from watersheds not grazed for at least 12 years are reported here.

Indices of soil nitrogen availability

Previous studies have estimated net mineralization of N in soil using buried bags (Ojima et al. 1990), and have reported concentrations in soil water on annually burned and long-term unburned prairie (Knapp and Seastedt 1986; Seastedt and Hayes 1989; Hayes and Seastedt 1990). Soil organic matter, total soil nitrogen and plant root nitrogen concentrations have also been routinely measured as part of ongoing Konza Prairie studies. In addition to summarizing those findings for this study, we report additional data relevant to documenting the effects of fire frequency on soil N availability. Soil water samples of NO_3^--N were obtained from porous cup lysimeters placed at 20 and 80 cm depths in the soil of a watershed burned every four years, and from lysimeters placed on three long-term unburned watersheds. Since root activity can complicate interpretations of N availability, only data from the March–April period, prior to the initiation of root growth of C_4 grasses, were included in our analysis. Nine lysimeters were located on each watershed; however, only some of these produced sufficient water samples for analysis in any particular year. Volume-weighted averages were obtained from each lysimeter, and a single composite estimate of soil water NO_3^--N was obtained from each watershed. Details of lysimeter design, sampling and NO_3^- analysis procedures have been reported in Seastedt and Hayes (1988).

Foliage biomass estimates

We used foliage biomass estimates obtained by the Long-Term Ecological Research (LTER) program to estimate differences in productivity on infrequently burned versus annually burned sites (Abrams et al. 1986; Briggs et al. 1989). Values reported here are means of oven-dried (60° C) mass of vegetation from 20, 0.1 m^2 clipped quadrats, taken in August from either cherty upland silty clay loam soils (Florence soils, Typic Natrustolls) or deep bottomland silty clay loams (Tully soils, Pachic Argiustolls). These soils differ appreciably, particularly in their water holding capacities. The deep soil, lowland sites tend to support higher plant productivity in most years (Abrams et al. 1986). Therefore, results are treated separately for each soil type. Five pairs of values (one year's data from one soil type, two years' data from two soil types) were obtained in this manner. One additional comparison was obtained from the report of Hulbert and Wilson (1983), resulting in six paired comparisons.

The above results may contain site as well as treatment differences (Hurlburt 1984); hence, we attempted a more rigorous analysis in 1989. Six 0.1 m^2 foliage samples were collected in late September from upland soils (Typic Natrustolls) on 10 annually burned and 7 less frequently burned (2 or 4-yr fire return frequency) upland sites. All sites were burned in mid-April of 1989. Sites for collecting samples were selected using a quasi-random procedure (blind quadrat toss). These samples were dried as before and composited into a single estimate of foliage biomass per site.

The variance associated with plant biomass estimates obtained from 0.1 m^2 samples is affected by burning treatment; production on unburned plots tends to be more variable when measured at that scale (Briggs and Knapp 1991). Rather than use a variety of statistical procedures, all statistical comparisons in this study were conducted using a nonparametric SAS t-test or ANOVA using ranked values. The F-statistics reported in the text are from the ranked data; however, nontransformed means and standard errors are given in figures.

Nitrogen fertilization experiments

A series of fertilization experiments were used to test the fire frequency -N limitation interaction. The first experiment (called EXP. 1) involved comparison of the production response of infrequently and annually burned prairie to "chronic" annual nitrogen fertilization. A series of 10 × 10 m plots were installed in 1986 on a site burned in 1985 to study the response of the prairie to a number of manipulations. The portion of the experimental design used here involved nitrogen additions to four pairs of annually burned and unburned plots. Fertilizer additions consisted of 10 $g \cdot m^{-2}$ of nitrogen as ammonium nitrate (NH_4NO_3). Annual plant requirements of N from the soil have been estimated at 4 $g \cdot m^{-2} \cdot yr^{-1}$ (Seastedt and Ramundo 1990); however, the microbial immobilization potential may have been sufficient to retain much of the first-year's application of N. Subsequent experiments (described below) therefore used twice as much N. Treatments have been applied annually in April since 1986. A total of 0.4 m^2 of above-ground biomass on each of the 16 plots was harvested by clipping quadrats selected quasi-randomly (blind toss method) at the end of each growing season. Foliage was sorted into living grass, living forbs (non-grass, non-woody vascular plants), and current year's dead (vegetation that had senesced prior to harvest). Statistical analysis of these data employed a randomized blocked design for fire, with N additions treated as a completely randomized experiment. The effects of fire were therefore tested with an ANOVA comparison using the block by fire interaction as the error term, while N effects were tested with the residual error term.

Two fertilization experiments were conducted in 1988. The first of these (EXP. 2) was conducted along a single upland plateau that runs the length of Konza Prairie and intersected a large number of watersheds, all of which were burned in the spring of 1988. Individual 1 × 2 m plots were randomly placed on six infrequently burned sites and on six annually burned areas. Half of each plot (1 m^2) was fertilized with 20 g of nitrogen as ammonium nitrate, NH_4NO_3. A 0.2 m^2 sample of foliage was taken from the center of each of the fertilized and unfertilized halves of these plots at the end of the growing season to estimate the foliage biomass response to the nitrogen additions. An estimate of the response of foliage to N additions was calculated from each paired plot using the formula, $[(F-C)/C]$, where F is the mass of vegetation from the fertilized half and C is the mass of vegetation from the unfertilized half.

A third study (EXP. 3) was established in early spring of 1988 to evaluate the effects of site history characteristics on the fertilizer-fire response. One set of plots was established on a site that, previous to the 1988 manipulations, had been burned annually for 16 years. A second set of plots was placed on a site that had not been burned for at least 19 years. Eight 100 m^2 plots were selected on each watershed. Half of these plots was selected at random to be burned, and each plot was subdivided into fertilized (20 $g\,N \cdot m^{-2}$) and unfertilized plots. A total of sixteen 0.2 m^2 quadrats was clipped in mid-September for each experiment and sorted into grasses, forbs and current year's dead. This experiment was repeated on the same sites in 1989. The statistical analysis used for these plots employed a two-factor factorial design, using the residual error term to test for main effects. A better procedure would have been to assess the fertilizer effect using a plot by fertilizer interaction term, but we lacked sufficient replication to do this. We therefore attempted a more robust analysis by creating a single relative difference term, $[(F-C)/C]$, as defined above, for each of the paired plots, and tested for a fire effect on this variable. In essence, this test addresses the question, "Is the fertilizer response mediated by burning?". Again, ranks were used in place of the actual values for statistical comparisons.

The last experiment (EXP. 4) was conducted in 1989 using watershed transects located on four watersheds, (annually burned, two year, four year and a long-term unburned watershed). Split 2 m^2 plots (20 $g \cdot m^{-2}$ N-fertilized, unfertilized) were established at approximately 20 m intervals along each watershed. Sample sizes varied from 20 to 28 split plots per watershed. A 0.2 m^2 quadrat was harvested in late July from the fertilized and unfertilized portion of each plot. These results differ somewhat from the other studies in that a variety of soil types and depths were included in the composite estimate for each watershed.

Rainfall amounts influence the patterns and relative differences in productivity of burned and unburned prairie (Towne and Owensby 1984). Relative production is higher on unburned prairie during drought years due to shading effects of litter and reduced evaporation of surface water. Rainfall was above average in 1986 and 1987. Rainfall was about 60% of Konza Prairie's 81 cm average in 1988, and again about 60% of average when vegetation was harvested on the LTER plots and watershed transects in 1989. By the time additional plots were harvested, late season rains resulted in 1989 being an average year in terms of the growing season precipitation.

Results

Soil N and soil water N availability in relation to fire frequency

A summary of available soil N data are reported in Table 1. Results indicate that N amounts in soil at Konza Prairie are not as yet different among fire treatments. Nitrogen mineralization rates and soil water nitrate concentrations are, however, a function of fire frequency. A time series of average soil water nitrates obtained in

Table 1. Comparison of soil nitrogen availability on annually burned and infrequently burned sites relative to long-term unburned plots

Variable	Percentage of values found on unburned plots		reference
	Annually burned	Infrequently burned	
Soil organic matter	95%	100%	a
Soil total N content	97%	94%	a
Net N mineralization	50%	125%	b
Soil water NO_3^--N (March–April)	65%	85%	a, c
Root N concentrations	62%	54%	b
Root biomass	120–170%	180%	a,b

[a] Seastedt and Ramundo 1990, and unpubl. LTER data

[b] Ojima et al. 1990

[c] Infrequently burned data shown in Fig. 2

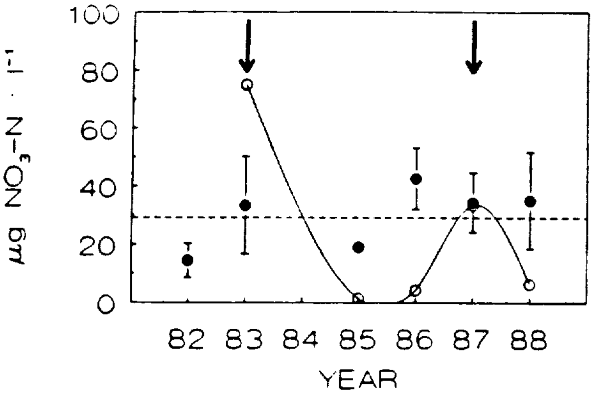

Fig. 2. March–April nitrate concentrations in soil water of long-term unburned watersheds (*solid circles*, $n=3$, *bars*=std. errors) compared with the average value for a single watershed burned every four years (*open circles*). Arrows indicate the years of burning in late April; the long-term average of the three long-term unburned watersheds is shown by the dashed line

March and April from lysimeters on a watershed burned in 1983 and again in 1987 compared to the averages from three long-term unburned watersheds exhibits the pattern predicted from the CENTURY model (Fig. 2). While the four-year burn experiment was not replicated, the site exhibited a decline in March–April soil water NO_3^- in years following burning, with levels recovering after three years of no fire to values observed on watersheds not burned for 10 years or more.

Production in relation to fire frequency

Peak foliage biomass estimates obtained from previous Konza Prairie studies indicated that, in the year of burning, infrequently burned sites generally have higher foliage biomass than that observed on annually burned sites. An analysis of all pre-1989 data from treatments paired by year and soil type indicated that production was 10.5% ± 3.5% (std error, $n=6$ pairs) higher on the infrequently burned sites. Samples collected in September 1989, also suggested this pattern. The average production was 270 ± 17 g · m^{-2} (std. error, $n=10$) on annually burned sites versus 326 ± 27 g · m^{-2} (std. error, $n=7$) on infrequently burned sites burned that spring, a difference of about 20%. This difference was not statistically significant (t-test of ranked data, $p=0.12$). Nonetheless, foliage biomass means of infrequently burned sites were higher than those of annually burned sites in six of seven paired comparisons (mean = 12%, range −2 to 20%).

Fertilization experiments

1. Chronic fire and N additions (Exp. 1). Burning and fertilizer additions to the same plots for four years had different effects on prairie productivity in different years (Fig. 3). No statistically significant effects for any treatment were observed in 1986. Burning significantly increased total foliage biomass in 1987 ($F=18.9$, df = 1,3, $p<0.03$), but not in 1988 ($F=0.0$). A strong interaction effect between N addition and burning was observed in 1988, with N additions having a greater effect on the burned plots ($F=16.2$, df = 1,6, $p<0.01$). In 1989, there was a strong fertilizer effect ($F=47.1$, df = 1,6 $p<0.001$), but no burning effect or interaction for total vegetation biomass ($F=0.3$ and 1.5, respectively). By 1989, however, forb biomass was substantially greater than grass biomass in the unburned, fertilized plots, and both grass and forb biomass exhibited strong fire-fertilizer interactions ($F=15.6$, $p<0.01$ and $F=11.9$, $p<0.02$, respectively).

Applying the formula, [(F–C)/C] to treatment means, the burned, fertilized plots averaged 67% more aboveground biomass per year than the burned, unfertilized plots over the four year experiment. In contrast, average foliage production on unburned, fertilized plots was only 19% greater than on unburned, unfertilized plots.

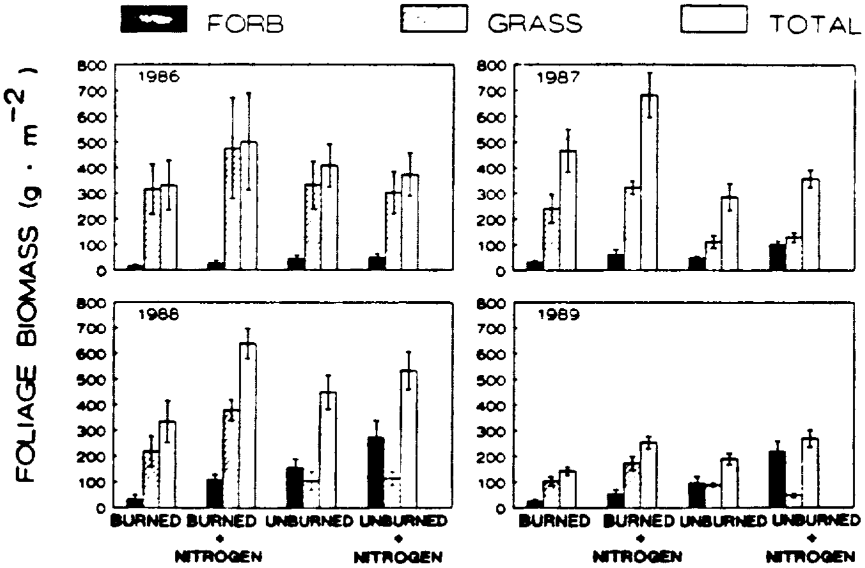

Fig. 3. EXP. 1. Response to nitrogen additions of forbs, grasses and total vegetation on burned and unburned prairie. Lines represent std. errors of 4 replicates per treatment

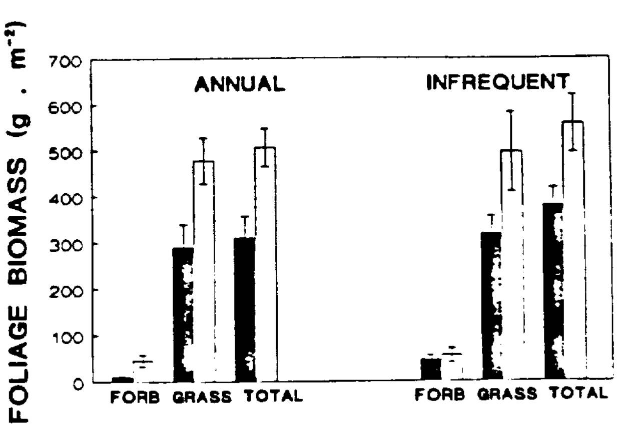

Fig. 4. EXP. 2. Fertilizer response *(open bars)* versus unfertilized plots *(solid bars)* for forbs, grasses and total foliage on annually burned and infrequently burned watersheds. Lines represent std. errors of six replicates per treatment

A suggestion of a temporal trend in the response of the vegetation to N occurred in both burned and unburned plots. Burned plots exhibited a 52% and 46% response in 1986 and 1987, respectively, but a 91% and 79% response in 1988 and 1989, respectively. The unburned vegetation response to N increased from essentially no response (−9%) in 1986, to 25% and 19% in 1987 and 1988, respectively, to 41% in 1989. These trends may have been induced by a cumulative reduction in microbial immobilization influences on the N additions, as well as by shifts in plant species composition due to chronic N additions.

The grasses on the unburned plots appeared less responsive to nitrogen additions than the forbs. By 1989, the grass response to N additions on unburned plots was negative due, perhaps, to competition by the forbs (Fig. 3). The forb response to N equalled if not exceeded that of the grasses regardless of fire treatment. Over the four year period, the average biomass of grass foliage on burned, fertilized plots was 57% higher than that on burned, unfertilized plots. In contrast, the forbs increased in biomass an average of 126% on burned, fertilized plots compared to burned, unfertilized plots. Thus, while fire was slowing the forb response to N additions, as indicated by the significant fire × fertilizer interaction in 1989, forb biomass on fertilized plots appeared to increase regardless of fire treatment.

2. *Effects of site history on the fire response.* EXP. 2 represented our only valid statistical test of the N response of infrequently burned sites burned in the year of study versus that of annually burned sites (Fig. 4). The tendency of infrequently burned sites to produce more biomass than annually burned sites was not statistically significant (*t*-test of ranked data, $p = 0.17$). The forb response to nitrogen addition was, however, affected by fire frequency ($F = 4.9$, $df = 1,10$, $p = 0.05$). Nitrogen additions to annually burned plots increased forb biomass from 8 to 37 $g \cdot m^{-2}$, but forb biomass was unaffected by N additions on the infrequently burned fertilized plots (59 vs 62 $g \cdot m^{-2}$, respectively).

The fire and N addition experiments on the long-term unburned and annually burned sites (EXP. 3) produced site-specific results (Fig. 5). We cannot compare these sites statistically; uncontrolled site effects such as soil depth undoubtedly influenced results. However, within-site results can be addressed. Both burned and unburned plots located on the long-term annually burned site exhibited strong responses to N additions in 1988 and 1989 ($F = 14.3$ and 9.0, respectively, $df = 1,12$, $p < 0.01$, Fig. 5A). Fire did not affect productivity on this site in either year ($F = 0.0$ and 0.7, respectively), nor did fire have a significant effect on the magnitude of the production response to N.

The second site used in EXP. 3, conducted on the long-term unburned watershed, demonstrated a negative fire effect in 1988 and a tendency toward a negative fire effect in 1989 ($F = 15.8$ and 1.8, $p < 0.01$ and $p > 0.05$, respectively, $df = 1,12$, Fig. 5B). Using the two-factor ANOVA on ranked data, neither N nor the N by fire interaction were statistically significant for either year. However, when the ranked value for percent increase due to N was evaluated for a fire effect, a significant response was observed in 1988 ($F = 6.9$, $df = 1,5$, $p < 0.05$) but not in 1989 ($F = 0.8$).

Fertilizer responses observed in EXP. 4, the four watershed transects measured in 1989, varied from a 16% increase to N enrichment on a long-term unburned site, a 27% increase on the four-year burn (burned in 1988), a 57% increase on the 2-year burn (burned in 1988), and a 48% increase on an annually burned site. These results, unlike the plot studies, integrate the effects that soil depth and soil type may have on N limitation patterns. While the magnitude of the N response on frequently burned sites was less than that observed in certain plot studies,

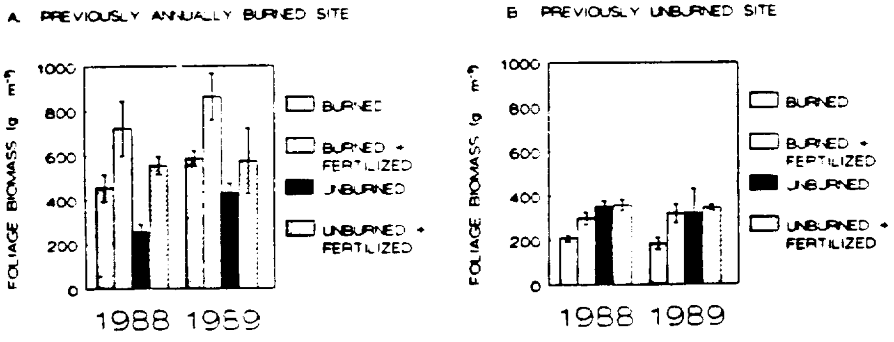

Fig. 5A, B. EXP. 3. Nitrogen enrichment to burned and unburned plots located on sites with an annual fire history (**A**) or unburned for about 20 years (**B**). Lines represent std. errors of 4 replicates

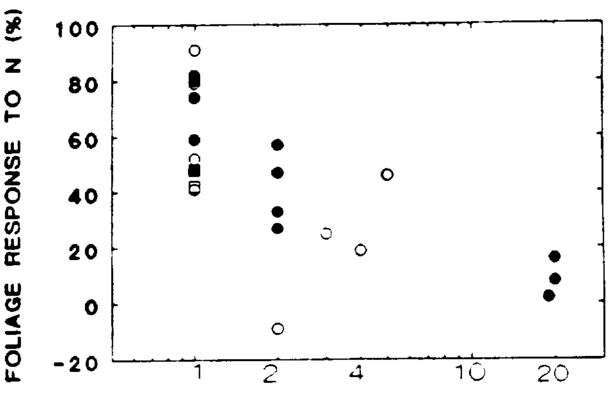

Fig. 6. Relative foliage response to N additions, summarized for all experiments, as a function of time since previous fire. *Open circles* represent data from the chronic N enrichment plots (EXP. 1) shown in Fig. 3. *Open squares* represent infrequently burned plots (EXP's 2, 3) burned in the year of measurement

the overall fire frequency – N response pattern was similar.

All results from EXP's 1–4 were graphed to observe the relationship between the time since the site was burned and the foliage production response to N additions (Fig. 6). Sites burned in the year of measurement were assigned x-axis values of 1, sites burned the previous year but not the current year were given values of 2, etc. The best linear model, using a log-transform of y-axis values, produced a highly significant negative relationship between plant response and time ($r^2 = 0.50$, $n = 22$). A model using both current year's fire status and time since the previous fire as a covariate produced a significant relationship for both variables and a combined r^2 of 0.64 ($n = 22$).

Discussion

Results generally support our four predictions regarding the extent to which fire frequency affects the degree of N limitation in tallgrass prairie. First, long-term unburned prairie, not burned in the year of measurement, is at most moderately sensitive to N additions. The average response to N additions from all long-term unburned sites was only 9% (Fig. 6, range 2–16%, $n = 3$). Second, annually burned sites (here, all plots burned in two or more consecutive years) were hypothesized to demonstrate maximum N limitation. Annually burned plots averaged a 68% increase to N (range 46% to 91%, $n = 9$). Infrequently burned plots were to exhibit an intermediate N limitation response, and these plots (burned within the last 4 years, and burned in the year of measurement) averaged a 45% increase to N additions (42% to 48%, $n = 2$). Finally, LTER records and our measurements made in 1989 on unfertilized prairie provide additional support for Hulbert and Wilson's (1983) observation that infrequently burned prairie produces more foliage during the year it is burned than annually burned prairie. Since all areas burned in the spring are presumed to have similar energy, temperature and moisture regimes, enhanced production on infrequently burned sites relative to annually burned sites must result from another source. Relatively high *N* mineralization rates on infrequently burned sites (Table 1. Ojima et al. 1990) are likely responsible for this phenomenon. At the time of burning of infrequently burned sites, soil water NO_3^- concentrations are relatively high (Fig. 2), apparently as a result of a decline in the input of root detritus with a high C:N ratio (Seastedt 1988; Seastedt and Ramundo 1990).

Interpretations of these results require several assumptions. We assume 1) that microbial immobilization potentials for N did not have major impacts on the observed foliage responses to N additions, and 2) that the foliage production response was not seriously compromised by treatment-induced shifts in root:shoot carbon allocation. Both of these assumptions appear reasonable. Annually burned sites should have the largest microbial immobilization potentials (Ojima 1987), yet these sites clearly had the greatest foliage production response to N. The chronic N addition plots (EXP. 1) received only half as much N per year as other plots, but, except for the first year's response, results appeared within the range of values observed for other experiments (Fig. 6).

Nitrogen fertilization probably affected root:shoot ratios, with relatively less production allocated to roots on fertilized plots (c.f. Huenneke et al. 1990). Root biomass measured in 1989 from the top 20 cm from the chronic N addition plots was not affected by N additions (Seastedt, unpubl. results), suggesting this was indeed the case. Assuming equal root production among treatments, then trends observed in the foliage should hold for the total plant response as well, although relative differences between treatments would be reduced.

Unburned prairie is, in years of average or above-average rainfall, less productive than burned prairie, and this response results largely from changes in the photosynthetic capabilities of the dominant species rather than major changes in the species composition of the prairie (Towne and Owensby 1984; Gibson 1988). Shading and cooling of the soil by litter reduce photosynthetic rates of the dominant grasses on unburned prairie (Knapp 1985). Chapin et al. (1986) reported that the community N limitation is influenced by the physiological status of the vegetation, as dictated by the age of the specific plants or by the species composition of the community. Here, age of the vegetation is assumed constant or unimportant, but, by self-shading, the vegetation has the potential to affect the strength of nitrogen limitation without changes in the species composition of the community. The build-up of surface litter and its subsequent mineralization, in conjunction with a reduction in root production from a less vigorous flora, increases the pool of available soil nitrogen, thereby modifying community N limitation through time.

Exceptions to our generalization that nitrogen additions have little effect on the productivity of prairie not burned in the year of measurement came from the unburned plots on the previously annually burned site

(Fig. 4A) and from the transect on the 2-year burned watershed conducted in 1989. The unburned plots in Fig. 4A were on a productive, deep soil site that had been annually burned for 16 years prior to the year of the experiment. While these plots were not burned in 1988, the consequences of severe N limitation induced by annual burning apparently carried over from previous years. In similar fashion, the 2-year fire frequency may also create chronic N limitations similar to those observed on annual burns. Old (1969) reported that a site not burned for three years was found to be more sensitive to N additions than a site burned that year. Previous fire history may therefore occasionally be as important as current burn status in determining the N response. The empirical model developed using data shown in Fig. 6 indicated that both current fire status and previous fire history affected the foliage response to N additions.

A major, albeit unexpected, finding of our research was the relative sensitivity of the forbs to nitrogen additions. This response had been reported for grazed pastures (Owensby et al. 1970; Owensby and Smith 1979), but such areas tend to have higher initial forb densities due to grazing activities. Recent work by Wedin and Tilman (1991) demonstrated that various tallgrass species strongly influence soil N mineralization rates as a consequence of the chemical and physical characteristics of their roots. They hypothesized that this phenomenon could affect competitive interactions and successional processes in grasslands. Frequent burning strongly favors the persistence of C_4 grasses over forbs and C_3 grasses (e.g. Gibson and Hulbert 1987; Gibson 1988), yet the mechanisms responsible for these shifts in plant community composition remain largely unknown. Because most forbs on Konza Prairie are C_3 species, we assumed that late spring burning gave the warm season C_4 grasses the competitive advantage to grow in a relatively warm, relatively dry environment. Findings from this study suggest that at least one of the mechanisms responsible for this response is the nitrogen limitation effect associated with frequent fire. When this relationship is decoupled using nitrogen fertilizer, forbs become more abundant, as observed in the 1986–1989 patterns from the LTER plots. This chronic N enrichment study was initiated for reasons other than those presented here. Nonetheless, the experiment is now useful to see if N enrichment rather than fire can control grassland succession, and to see if grasslands exhibit the same responses as do forests to chronic N additions (Aber et al. 1989).

Acknowledgments. The questions addressed in this study were generated by predictions from the CENTURY model as modified by Dennis Ojima, William Parton and David Schimel. Tim Todd provided the statistical design for the LTER Plots. Comments from F.S. Chapin III, James Clark, Beth Holland, Alan Knapp, Clenton Owensby and an anonymous reviewer substantially improved earlier drafts of the manuscript. Lisa Armstrong, Jenny Brazzle, Brent Brown, Stacy Cloughley, Thomas Haner, Patrick Hays, Keith Hayward, J.D. Jasper, Diane Jennings, Bryan Jones, Lisa Smith and Wendy White prepared plot treatments, clipped quadrats, sorted vegetation and encoded data. Rosemary Ramundo supervised field and laboratory analyses. Tracy Benning provided the 1989 transect data as part of a combined NASA and NSF research project funded through Colorado State University. These data and supporting documentation are stored in the Konza Prairie LTER data base., Enquires about the use of these data should be sent to the Data Manager, LTER, Division of Biology, Kansas State University. Research has been primarily supported by Long-Term Ecological Research grants from the National Science Foundation to Kansas State University.

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Chapter 9

LONG-TERM ECOLOGICAL QUESTIONS AND CONSIDERATIONS FOR TAKING LONG-TERM MEASUREMENTS: LESSONS FROM THE LTER AND FIFE PROGRAMS ON TALLGRASS PRAIRIE.

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Long-Term Ecological Questions and Considerations for Taking Long-Term Measurements: Lessons from the LTER and FIFE Programs on Tallgrass Prairie.

T.R. Seastedt and J.M. Briggs

> "We have just enough time left in this century to achieve a major new synthesis and understanding of the Earth System..." (NASA 1988)

9.1 INTRODUCTION

The earth, with its global problems of overpopulation, over-use and abuse of fossil fuel and nuclear energy, and production of toxic wastes, has often been compared to a sick patient. Illness is recognized as a significant deviation from known, long-term trends. Long-term monitoring represents a minimal activity for responsible individuals and agencies interested in placing current environmental problems into perspective. Long-term measurements are directed at questions involving phenomena not interpretable or perhaps not useful when viewed over short (annual or less) time scales, but are related to the long-term "health" or functioning of the system. At a minimum, the Long-Term Environmental Research (LTER) data therefore provide the context in which short-term observational or experimental results can be interpreted (Magnuson, in press). A much more interesting, albeit potentially less relevant use of LTER data involves the study of a set of complex questions that cannot be resolved with short-term studies (Franklin, 1989; Tilman, 1989). The juxtaposition of basic and applied science within the context of a single research effort is a strength of the LTER program.

This chapter attempts to identify a set of long-term ecological questions that are useful to a national or international network of research sites. While there exists a nearly infinite list of interesting questions that could be addressed with long-term studies, a realistic and goal-oriented list of measurements is presented. The criteria for selecting these questions involved identifying variables that 1. are useful for intersite comparisons, 2. are not strongly biased by spatial scaling factors, and 3. can provide the necessary linkages between atmospheric/climatological variables and biological measurements. "Focused studies of the interactions between the atmosphere and the biosphere that regulate trace gases can improve both our understanding of terrestrial ecosystems and our ability to predict regional- and global-scale changes in atmospheric chemistry" (Mooney *et al.*, 1987). The list of proposed variables for study was developed from the "core LTER measurements," a guideline used since the inception of the LTER effort (Callahan, 1984) from recommendations suggested in Earth System Science (NASA, 1988), and from practical experience with the recent NASA-ISLSCP (International Surface Land Climatology Project) conducted on the Konza Prairie LTER site (Sellers *et al.*, 1988). While appropriate examples are taken from many systems, particular emphasis has been given to questions that have interested researchers studying grasslands. We build on the work of Strayer *et al.* (1986). Their extensive overview of long-term studies provided useful definitions of research productivity, of what constitutes "long-term research," and reasons for the "successes" of previous and existing long-term research efforts. Their findings emphasized that individual scientists and not specific research protocols or experimental designs were largely responsible for successful long-term research efforts. Here, however, we suggest that certain constraints on research designs are important if a goal of the research is to benefit directly a regional or global network.

9.2 APPROPRIATE OBJECTS FOR LONG-TERM NETWORK MEASUREMENTS

The five core areas of the LTER include studies of the following topics (Callahan, 1984):

-Spatial and temporal distributions of populations,

-Patterns and frequency of disturbance,

-Pattern and control of primary production,

-Pattern and control of organic matter accumulation, and

-Patterns of inorganic input and movements through soils.

While excellent research has been done on some or all of these topics at one or more of the LTER sites, current efforts of linking sites in regional or global networks suggests that certain measurements are likely to be more useful than others.

Many of the most interesting and useful empirical studies of individual species have been long term in nature (Iker, 1983; Strayer *et al.*, 1986). For example, Weaver (1954) documented the response of the North American prairie species to climate and grazing intensities observed over a 40-year interval in the first half of the 20th century. The rainfall and temperature conditions under which these studies were made are exemplified by data obtained for the Manhattan, Kansas, area (Figure 1). These data show that the great drought in North America during the 1930s was accompanied by (and contributed to) relatively high ambient temperatures. During the drought, Weaver documented the eastward advance and expansion of xeric, shortgrass species at the expense of mesic, tallgrass vegetation. The return of relatively wet years in the 1940s reversed this trend. The annual values of temperature and precipitation shown in Figure 1 indicate that "average" conditions for the prairie cannot be expected without an approximately 20-year record. Even then, the factors that govern patterns of species composition and abundance may be misinterpreted or overlooked. Weaver (1954), for example, did not appreciate or acknowledge the role of fire in suppressing the invasion of woody species onto the tallgrass prairie, nor did he notice that the productivity of the dominant species was often enhanced by frequent fires.

Studies of within- and between-habitat species diversity remain of keen interest to many ecologists. Nonetheless, we suggest that individual species, species lists, or indices derived from species lists make poor primary intersite comparison measurements. Many species are not found across large environmental gradients. Those species that do cover regional areas are not physiologically identical across these regions. The relevant units to address intersite comparisons should confer equivalency across sites, and these units should aggregate into meaningful values at different spatial scales. Energy and mass (including elements, trace gases, etc.) are obvious candidates for study. Biologists must still focus on the biota as cause and effect participants in energy and mass transformations, but both the forcing functions and the response variables must employ units common to all sites. Eventually, life history characteristics and physiological responses of the individual species will provide a mechanistic interpretation of site-specific responses. Even then, however, these responses will be governed by spatial patterns not often measured in population studies (Huston *et al.*, 1988).

All LTER sites have been charged with studying "disturbance" as a core measurement. Our own experience with this topic has suggested serious problems associated with the concept that may prevent "disturbance ecology" from becoming a major tenet of ecological theory (Evans *et al.*, in press). One problem has been the popularity of the topic, and the inevitable misuse of the term that comes with popularity. "Disturbance" is used simultaneously to describe a system input (e.g., a storm) and system output (e.g. species die-off) (Rykiel, 1985). Obviously, the latter is the interaction of the system with an input, and is therefore very much a characteristic of the system while the former is uncontrolled by the state of the system. A second problem with disturbance theory is that identical inputs can produce very different outputs depending upon the initial state of the system and the scales at which the output is measured. For example, fire adversely affects a number of populations of plants and animals in the tallgrass prairie. Nonetheless, certain species are benefited and periodic fires are required for the perpetuation of the system. Is fire or the absence of fire the disturbance in this system? Can systems lacking stable equilibria be disturbed? System-level properties of resistance and resilience to disturbances can be viewed more logically and mechanistically as consequences of structural and life-history characteristics of biological systems. Different disturbances (fire, drought, grazing, etc.) produce very different species and system responses. Konza Prairie researchers found the discussions about species and ecosystem responses to "disturbances" to be largely an exercise in after-the-fact descriptive ecology and a topic not conducive to the development of predictive models. A much more productive approach to generic disturbance-type questions involves explicit identification of forcing functions and the responses of the system at specific levels of resolution. In other words, we believe that the LTER core area involving disturbance can be adequately addressed within the context of studies focused on the other core areas. This is certainly true in grasslands and agroecosystems where studies use fire, grazing, or tillage practices as experimental manipulations.

The remaining three core areas of the LTER program (net primary production, organic matter, and nutrient dynamics) provide a logical, unified focus for regional and global networks. These core areas employ units that are constants and provide the direct links between biotic and atmospheric processes. A combination of relatively new, spatially explicit measurements, in conjunction with traditional methodologies, will allow ecologists to study biota-climate interactions while concurrently focusing on questions of local interest.

9.2.1 Primary Productivity

Forested sites have considerable potential to demonstrate the linkages among net primary productivity, trace gases, and climatic changes. Dendrochronology studies have used annual woody growth increments to reconstruct recent past climates. Other studies have combined paleobotany, records of lake ash deposition, and dendrochonology to reconstruct forest species composition, fire frequency, and growth relationships. Clark (1988) demonstrated the relationship between climate and fire frequency which, together, shaped the species composition and productivity of the north temperate forests. Of particular interest has been the work of LaMarche *et al.* (1984) which suggests that subalpine forests in western North America began to alter their growth patterns with respect to climatic variables sometime in the 1960s. Those authors suggested CO2 enrichment as a possible factor. Anthropogenic sources of nutrients in bulk precipitation could, perhaps, be an alternative hypothesis. Regardless, the measurement of woody growth and, therefore, a record of the past productivity is possible at many sites, and is a reasonable, partial index of aboveground net primary productivity. Such data are particularly desirable since 1. sampling can be accomplished on a very infrequent, year-to-decades basis, 2. large sample sizes can be obtained and potentially interacting variables (soils, species, etc.) can be evaluated, and 3. the samples can be easily archived so that future analyses or reanalysis of the same, original data set are possible. To complete the story of aboveground productivity, foliage production should be measured. Litterfall or needle production measurements and procedures are common, but should be supplemented, if possible, with satellite-derived digital images. These images can provide a spatial perspective not possible with microplot measurements, and the types and uses of currently available satellite images are discussed below.

Retrospective analyses of grassland productivity cannot be as easily accomplished as forest studies. Sedimentation rates of glacial lakes, in conjunction with pollen analyses, may provide some useful historical data. Also, carbon isotope studies of sediments, soils (including paleosols), and groundwaters in conjunction with these or other research may also provide an interesting story, particularly with respect to changes in the composition of C3 and C4 plants (O'Leary, 1988).

More recent retrospective analyses of indices of grassland productivity can also be conducted using the satellite imagery. Researchers and sites should move quickly to secure these images lest useful information be lost by agencies not funded as data archives. A listing of potential data sources (Table 1) indicates the resolution and information available from each type of satellite. Investigators need to be aware of the various trade-offs involved in using these various types of data, and some important considerations are outlined in Sellers *et al.* (1988). In general, we believe that the high spatial resolution (small pixel size) of the Landsat TM or SPOT satellites is extremely useful in evaluating within-site topoedaphic or experimental (fire or grazing) effects. However, a seasonal time-series of these types of data is expensive or simply unlikely to be obtained due to relatively infrequent overflights in conjunction with moderate to high probabilities of cloud cover. In contrast, the NOAA-AVHRR satellite provides relatively low spatial resolution (large pixel size) but high temporal resolution, making cross-site, cross-year, and seasonal comparisons possible. The potential for using these images as analogs of regional productivity and for estimating trace gas interactions and energy exchange is just beginning to be developed. Recent improvements of algorithms, particularly those employing the vegetation index (Tucker *et al.*, 1985; Goward *et al.*, 1986) or some combination of the vegetation index in conjunction with thermal measurements (Forrest Hall *et al.*, unpublished results) can demonstrate both seasonal and long-term trends in plant biomass and plant vigor. We expect that the more sophisticated, high resolution imaging spectrometers scheduled for space orbit in the near future will provide more useful data for measuring both biomass and plant productivity at moderate scales. This enhancement begins with the anticipated 1991 launch of Landsat 6 with the Enhanced Thematic Mapper (ETM) on board. Eight bands of spectral information are planned, four in the visible (one being a 15 m pixel panchromatic), two in the near-infrared, and two in thermal portions of the spectrum. This system is reported to be very sensitive to surface temperature changes and should, therefore, be very useful in relating vegetation dynamics to energy dynamics. Subsequent satellite equipment scheduled for the Earth Observing System (EOS) program will make considerable advancements in the spectral resolution of these digital images. These standard products could also be supplemented with aerial photography, including standard panchromatic, color, and color IR images. Photographic records are proving useful for a variety of retrospective analyses.

9.2.2 The Interaction Between Productivity and Surface Climate

A conceptual model developed by Shugart (1986) (Figure 2) suggests how we might think about the relationship of LTER measurements to studies involved in trace gas fluxes. The latter measurements are, by necessity, made on a scale that detects strong diurnal and seasonal fluctuations. In contrast, LTER measurements of NPP, organic matter, or elements have a much coarser temporal scale. However, as suggested by the model, these long-term ecological processes function as constraints on short-term physiological processes, and therefore mediate the response of vegetation to climate. We present an example of this phenomenon to emphasize the need to recognize that changes in ecological constraints such as fire frequency, herbivory, or, nutrient availability may temporarily overshadow direct changes in temperature or rainfall.

Our data on temperate grassland plant productivity demonstrate a strong relationship between the type of management treatment and productivity (Figure 3). The tallgrass prairie requires periodic fires to maintain its species composition and productivity (Knapp and Seastedt, 1986). In average or wet years, annual burning in late spring benefits the C4 grasses. However, some but not all drier than average years result in more productivity by the combination of C4 and C3 grasses, forbs, and woody species found in the unburned prairie. Following a fire, the blackened soil surface of burned prairie is exposed to direct solar radiation and converts much of this energy into sensible heat absorbed by the soil (Figure 4). However, by midsummer, the re-establishment of the canopy, in conjunction with greater rates of evapotranspiration, results in a cooler soil surface. This pattern is reversed at the 10 cm depth, where the drier soils on the burned sites lack the thermal inertia of generally moistened, litter-covered soils of the unburned sites. The greater rates of evaporation coupled, perhaps, with higher rates of reflected infrared radiation keep burned areas cooler in midsummer than unburned areas (Figure 5). The thermal (channel 6) Landsat TM image in Figure 5 shows that the radiometric brightness on burned watersheds is, on average, less than that measured for adjacent unburned areas (Figure 6) (Asrar *et al.*, 1988). These data demonstrate that the ecological constraints operating on the vegetation (here, a spring fire) influence both the hydrologic and energy budget. These changes are detectable at both a micro- and macro-scale level. Obviously, a change in the fire frequency of relatively large tracts of grassland could have an impact on the regional climate.

Grazing by cattle also had a measurable affect on canopy temperatures as measured by the radiometric brightness of the TM image (Figures 5 and 6). Grazed areas were cooler in August, presumably because the grazed vegetation was physiologically more active than a similar amount of ungrazed vegetation and was transpiring relatively greater volumes of water. Consumers affect both the amounts and physiology of the vegetation and thereby can greatly alter vegetation-climate interactions, particularly in grasslands. Investigators should also be aware that interactions between energy and nutrients may affect consumers, so that consumers become important transient controlling factors on net primary productivity (White, 1984). These controls can operate directly via consumption of plant parts or indirectly by controlling plant species composition (Schowalter, 1981). Thus, knowledge of consumer populations may contribute to an understanding of vegetation-climate interactions. This observation also has particular relevance in agroecosystems, where biotic mechanisms of consumer regulation have been severely altered.

9.2.3 Nutrients

Virtually all LTER sites measure nutrient inputs, standing crops, and outputs. The input data may be restricted to analyses of wetfall, often associated with the National Atmospheric Deposition Program (NADP). This measurement is often inadequate because dryfall deposition or deposition associated with dew can be considerable (Lindberg *et al.*, 1986). Most sites obtain pH measurements in conjunction with the inputs of nitrate, ammonia, sulfate, and the major cations. Measurements of the standing crops of the major elements in vegetation were initiated at many sites during the International Biological Program. It is to be hoped that such data have been archived for future analyses or as baselines for future comparisons. Our site archives plant and soil samples along with the numerical data, and this procedure has received endorsement by other research groups (Pace and Cole, 1989). To our knowledge, no LTER site has engaged in long-term monitoring of net inputs or outputs of trace gases (CO2, NOx, NH3, H2S, or SO2). However, with the advent of large path-length infrared spectroscopy (Gosz *et al.*, 1988), and procedures to estimate fluxes, this deficiency should be resolved, at least at a few sites. Moreover, as mentioned above, the trace gas fluxes are diurnal phenomena operating under the ecological constraints being studied by the LTER. Empirical results and modeling efforts currently underway as part of FIFE (First ISLSCP Field Experiment) at Konza Prairie should be able to tell us the relationships and sensitivity of measurements such as productivity to short-term and seasonal estimates of gas flux.

Nutrients become constraints on plant growth during periods when energy and water are not limiting, i.e., under conditions otherwise favorable for plant growth. An obvious question of interest to those involved with climatic change studies is the extent that nutrient limitations may mediate vegetation responses to enhanced CO2 (Tissue and Oechel, 1987). If plant growth is nutrient as opposed to energy limited, then carbon dioxide enrichment and/or increased temperatures should not immediately affect productivity. In tallgrass prairie, an improved energy environment (created by fire) results in a higher nitrogen use efficiency (NUE) of the vegetation (Ojima, 1987). With this greater production, however, comes increased detritus build up and nutrient immobilization. In several biomes, including the taiga (van Cleve *et al.*, 1983) and tallgrass prairie (Knapp and Seastedt, 1986), plant litter has a direct negative physical effect on energy availability to plants. Detritus production could, therefore, affect productivity both by affecting usable energy inputs and by influencing nutrient availability. Seasonal shifts in energy, nutrient, and water limitations, in conjunction with negative feedbacks resulting from biomass production, prevent these ecosystems from maximizing their production responses.

The need for long-term nutrient measurements relates to the fact that climate can influence both amounts and availability of nutrients. For example, the rainfall data shown in Figure 1 indicate that precipitation at the Konza Prairie LTER site was above normal for the period 1981 to 1987. Accordingly, plant productivity was above the long-term average during this interval. Since inorganic nitrogen availability in soils is inversely related to the amount of "new" fixed carbon present, the organic matter build-up during this interval undoubtedly adversely affected inorganic nitrogen availability to plants. Generalizations about nitrogen availability and cycling and its importance to vegetation made during this wet interval are therefore biased and potentially incorrect, in spite of a seven-year data base.

Agroecosystems have additional nutrient inputs and outputs not found or not important in natural systems. Nutrient supplements from fertilizers and outputs in the form of harvested plant parts tend to create an artificially dynamic system. Areas employing irrigation also have potential additional exports of trace gases or leaching losses, and certain agricultural practices, such as conversion of largely aerobic, vegetated sites to largely anaerobic rice fields, are probably having a large effect on trace gas dynamics (Mooney *et al.*, 1987). A detailed accounting of these nutrients is warranted given the progressive enrichment of groundwaters with undesirable organics and nitrates. Moreover, the tillage of the soil, the artificial, excessive harvesting of plant nutrients, in conjunction with applications of supplemental water and fertilizers, have created unique situations of nutrient limitation, soil acidification and aluminum toxicity problems for agricultural systems (Adams, 1984). Indeed, many sites have been so totally altered by intensive agricultural practices that moderate changes in temperature, rainfall, rainfall chemistry, or rainfall pH would appear of secondary consideration relative to the direct human manipulations. The relevant emphasis from a network standpoint is, therefore, not how these systems are affected by climate change scenarios, but rather how the systems are affecting regional energy and trace gas dynamics. The ecological constraints of agroecosystems are the crop and tillage manipulations. These, like fire and grazing in the prairie, control the system interactions and responses to climatic inputs. Measurement of nutrient outputs from ecosystems has proved to be an extremely relevant and useful long-term index of integrated system behavior. Likens *et al.* (1977), Likens (1983) and Driscoll *et al.* (1989) have provided ample examples of these measurements. Their 25+ year effort on the relationships between nitric and sulfuric acid rain inputs and stream pH and stream nutrient responses comprises some of the most relevant and important ecological research of this century. Ironically, this work began with some focused, short-term experimental studies, but the utility of these measurements for questions requiring a longer study period became obvious shortly after the initiation of the experiments. Stream chemical analyses have provided a measurement of the integrated ecosystem response to changes in atmospheric inputs or to changes induced by within-system manipulations. In similar fashion, the new generation of remote sensing equipment scheduled for earth orbit within the next 10 years should provide equivalent information for terrestrial systems. Multispectral scanner, high-resolution sensors will provide a spatially explicit measurement of the integrated landscape response to changes in atmospheric inputs and landscape manipulations. Certain chemical properties of vegetation such as water status and nitrogen content can already be measured to some extent with current satellite data (Rock *et al*,. 1986; Waring *et al*., 1986).

9.2.4 Organic Matter

Plant detritus and soil organic matter provide the major reservoir of nutrients in most terrestrial ecosystems. This storage component provides the "resistance" of the system to changes caused by the destruction of the vegetation. The tropics-to-taiga gradient in organic matter is an example of the interaction between net primary productivity, decomposers, and climate (Swift *et al*., 1979). Any brief interpretation of this pattern is an oversimplification. Nonetheless, plants appear to have dealt better with climatic restraints than have the decomposers. In the United States the east-to-west gradient in soil organic matter observed across the prairie is largely controlled by moisture (Jenny, 1930). Prediction of changes in the organic reservoir, therefore, potentially depends upon the interaction of temperature and moisture, and the net effects that these variables have on production and decomposition (Hunt *et al*., 1988). Soil organic matter measurements tend to be rather insensitive to short-term manipulations of productivity and decomposition, but should be useful monitors of long-term changes (Jenny, 1980; Ojima, 1987; Ojima *et al*., 1990). Moreover, such data are generally available on a regional basis, and have been modeled very successfully using climate and management constraints as forcing functions (Parton *et al*. 1987a, b).

Investigators need to recognize that edaphic factors and climatic variables produce interaction effects that add to the complexity of regional patterns. A recent example is from Sala *et al*. (1988). That study found that sites with coarse, sandy soils were relatively more productive than fine, clay soils under below-average rainfall, while clay soils were relatively more productive under average or above-average rainfall. The coarse soils lacked the fertility of fine soils, but tended to allow water to penetrate below the zone of evaporation. Hence, the variability in productivity in coarse soils was reduced (i.e., productivity in wet years was diminished while the consequences of drought years were less severe). This phenomenon, when linked to a climatic gradient, produces a complex pattern (Figure 7). The relevance of these findings to models linking ecosystems to global climatic models should be particularly obvious.

9.2.5 Scaling and Sampling Considerations

The problem of how to integrate point measurements so that these data can be useful and accurate estimates of regional dynamics remains unresolved. A large literature on scaling is developing (Allen *et al.*, 1984; Urban *et al.*, 1987). By far the most productive approach we have seen involves the use of explicit spatial models to aggregate ecosystem processes (Huston *et al.*, 1988). Successful large-scale regional models of net primary production, nutrient cycling, and organic matter dynamics have to date employed a coarser approach based on the ecological constraints of climate and soils (Parton *et al.*, 1987a,b). However, plans are underway to interface the fine-scale, spatially explicit models as inputs to the larger scaled models (Shugart, this volume). We believe that a minimum of a two-step approach (organismic to ecosystem process level phenomena and ecosystem to global climatic models) will be required. Successful models will include those that adequately portray the operation of temporal and spatial ecological constraints on biotic processes.

Inputs required for global scale models may require large spatial resolution but fine temporal resolution. As discussed above, such data will probably use satellite data and algorithms developed from FIFE-type projects (Sellers *et al.*, 1988). Our own work with that project has convinced us that certain characteristics measured at small plot scales can be directly related to larger scale measurements (Figures 3 to 5). These measurements can be scaled up to function in input-output relationships with large-scale climate models. However, large errors will be introduced if the ecological constraints (i.e., land management) contributions are not included. In our region, changes in the ecological constraints to net primary productivity, i.e., changes in fire frequency or grazing intensity in prairie or changes in cropping and tillage practices in agroecosystems, will alter these algorithms.

Rules for minimum sample frequency and minimum sample size must be developed, based on knowledge of the underlying population variance (Wiegert, 1962; Kimmons, 1973; Greig-Smith, 1983). Investigators must decide what constitute significant shifts in their systems given the intrinsic level of variability. This analysis is relatively straightforward for time-series measurements that are assumed to be measured without error or that have no within-site variance component. For example, given our current precipitation data base (Figure 1), annual rainfall at our site must deviate by about 50 percent of the mean before we have an "unusual" wet or dry year (i.e., assuming a normal distribution, outside of the 95 percent confidence). For each measurement, investigators can calculate the necessary sample size needed to detect statistically significant differences given hypothetical differences in population means with known or estimated population variances. Consider the problems associated with measuring export of nutrients from two watersheds (Figure 8). In the Dismal River system, a few baseflow samples accompanied by a storm-event sampler should produce a very accurate measure of export. The lack of inherent variability and high degree of predictability in flow from this sandhills prairie makes detection of slight changes in mean values or changes in the magnitude of annual variations a potentially easy task. In contrast, the Blue Beaver Creek system in Oklahoma exhibits extreme variability and little predictability. Stream discharge appears to be largely controlled by surface runoff in this mixed-grass drainage. The ability to show some statistically significant change in export in this system as a result of changes in land management or climatological inputs would be difficult if not impossible for studies shorter than a decade in duration. Likens (1983) discussed similar problems for measuring element and ion export for Northeastern U.S. streams.

On a regional basis, the variability in stream flow appears to be correlated with the variability in annual foliage productivity. Figure 7 illustrates that the source of the Dismal River, the sandhills of Nebraska, is a relatively more stable environment for plant production than the drainage area of Blue Beaver Creek in the western plains of Oklahoma. This variability, itself, can become a long-term measurement, and analyses such as those conducted by Sala *et al.* (1988) should identify sites that have intrinsically lower variability. For studies interested in evaluating directional changes, low variability and high predictability appear to be a desirable characteristic. The Sala *et al.* data also demonstrate the need for a large number of sites to characterize the regional response to year-to-year climatic variability.

9.3 DOCUMENTATION AND DATA BASE MANAGEMENT

The value of creating permanent plots, adequately documenting procedures, and creating a user-friendly data base cannot be overemphasized. With few exceptions, data bases have not outlived the investigators who collected them (Strayer *et al.*, 1986). Those that have survived have become ecological treasures. Tilman (1989) noted that about 90 percent of all field studies are three years or shorter in duration. Even these short-term studies, if adequately documented and site referenced, could be subsequently resampled for similar or other ecological questions. We believe that we have lost many thousands of dollars worth of valuable data because a number of ecological studies with a "short-term focus" were not well documented on our site. Since those projects were terminated, we have come up with a number of questions that could have been addressed using the original data if we could only locate the site where the original measurements were obtained. A similar argument can be made for user-friendly documentation of the data. We have found a variety of new questions for old data sets. These data can be quickly retrieved and reanalyzed, even in the absence of the individual(s) responsible for the original data set. One cannot be serious about measuring decade-to-century-level phenomena without making a serious time and financial commitment to documentation. Researchers are referred to Gurtz (1986) and other references in Michener (1986) for excellent guidelines in this area.

9.4 CONCLUSIONS

The recent Earth System Science Report (NASA 1988), in its recommendations and review of ongoing and proposed research for the IGBP, concluded, "The overwhelming importance of sustained, long-term measurements of global variables emerges clearly from these studies" (page 137). We contend that a subset of the LTER core measurements, NPP, nutrients, and organic matter dynamics are particularly appropriate for relating vegetation dynamics to surface climatological measurements at a regional or larger scale. Biophysical measurements obtained from small plots, measured under known ecological constraints, will scale up in a fashion conducive to the modeling approaches suggested by Urban *et al.* (1987) and Huston *et al.* (1988). In our region, these ecological constraints include the fire and grazing regimes of the grasslands, or the particular management practice imposed on agroecosystems. We do not mean to ignore biodiversity efforts, and emphasize that individual organisms are driving the spatially explicit site responses (Huston *et al.*, 1988). Nonetheless, these effects must be translated into biophysical rather than simply biological units to be useful at the intersite level.

9.5 ACKNOWLEDGMENTS

We thank M.E. Gurtz, U.S. Geological Survey, for the stream examples. Ideas about ecological constraints developed from discussions with D.S. Schimel. Climatic data was provided by Dr. Dean Bark. We appreciate a review of an earlier draft of this manuscript by A.K. Knapp and C.L. Turner. Support for our research and the preparation of this effort was provided by the National Science Foundation (BSR-8514327) and NASA (NAG-5-897) grants to Kansas State University.

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FIGURE LEGENDS

Figure 1. Deviations from average annual precipitation (A) and mean maximum temperatures (B) for an area near Manhattan Kansas and the Konza Prairie LTER site. The data are for the period 1891-1987. Note that the temperature maxima corresponded with low precipitation values during the 1930s.

Figure 2. Conceptual model by H.H. Shugart suggesting the relationships between LTER-type measurements (right side of figure) and those variables strongly influenced by diurnal variations (left side of figure).

Figure 3. Time series of maximum foliage production on annually burned and unburned prairie. Year-to-year climatic fluctuations affect the vegetation response to treatment.

Figure 4. Weekly mean minimum-maximum soil temperatures in summer 1987 for burned (solid lines) and unburned (dashed lines) tallgrass prairie at 2 cm and 10 cm soil depths. Note that temperatures are relatively cooler on the burned site at 2 cm but are relatively warmer at 10 cm.

Figure 5. A Landsat TM thermal (channel 6) photo of Konza Prairie. Watershed boundaries have been superimposed over the image. Burned watersheds or grazed pastures are distinguishable by the darker pixel values.

Figure 6. Means and standard deviations of pixel values of radiometric canopy brightness obtained from Figure 5. All treatments exhibit statistically different values.

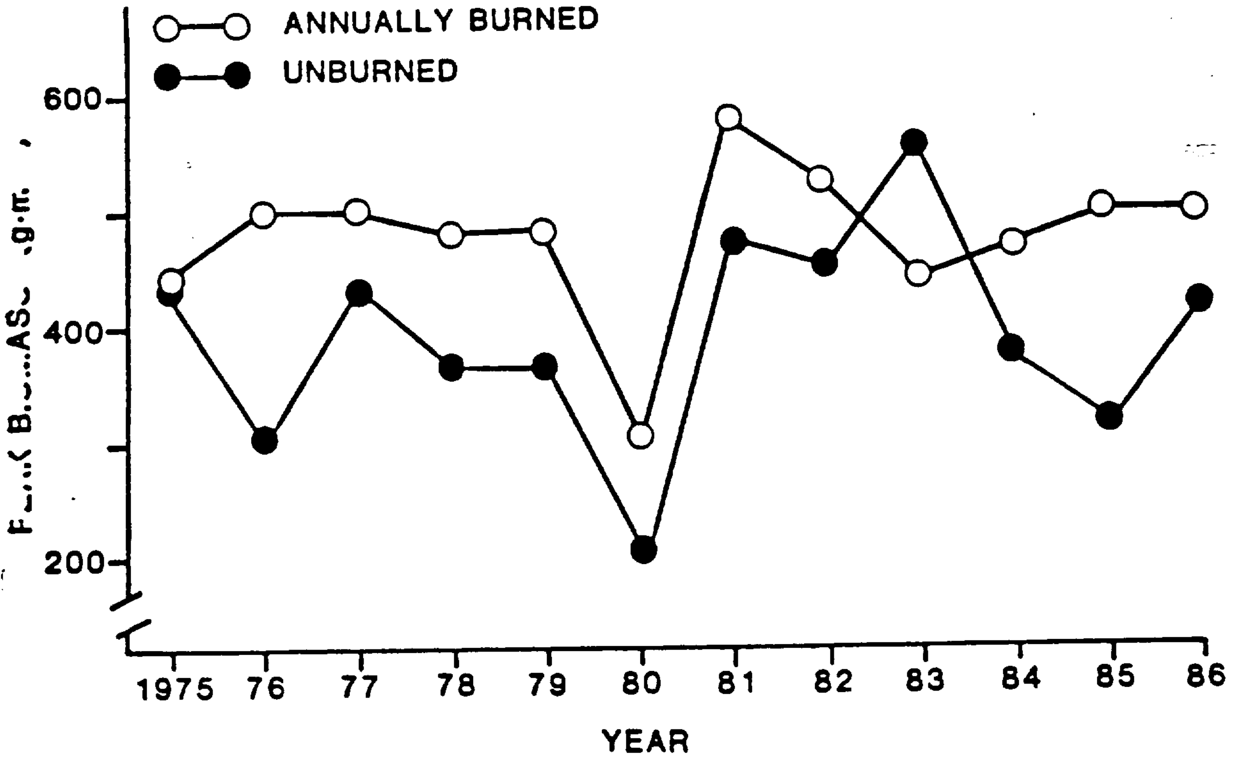
Figure 7. An 18-year record of maximum monthly streamflow from two US Geological Survey Benchmark watersheds. (data courtesy USGS).

Figure 8. Variation in foliage production in the central US (Mean values of good years minus mean values in bad years, divided by the overall mean). Reproduced with permission from Ecology (Sala et al., 1988).

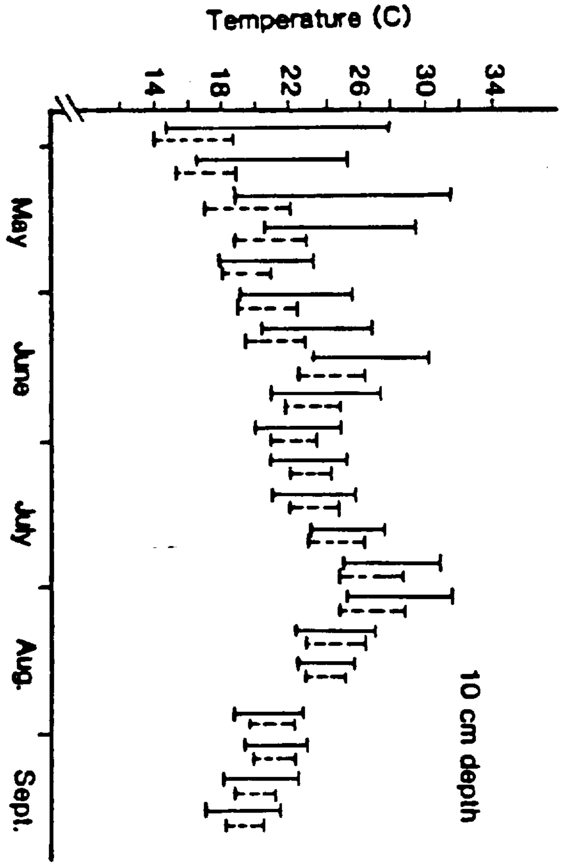
TABLE 1. Characteristics of current satellite imagery.[1]

Satellite	Pixel size	Return time	Comments/ example of users
NOAA AVHRR	1.1 km	daily	5 channels with 3 thermal bands Tucker et al. (1985)
Landsat MSS	80 m	16 days	4 channels with no thermal bands White and MacKenzie (1986)
Landsat TM	30 m	16 days	7 channels with one thermal band Ustin et al. (1986)
SPOT	10 m, 20 m	programable, 26 day nadir	10 m pixel panchromatic, 20 m pixel 3 channels, no thermal measurements Hardisky et al. (1989)

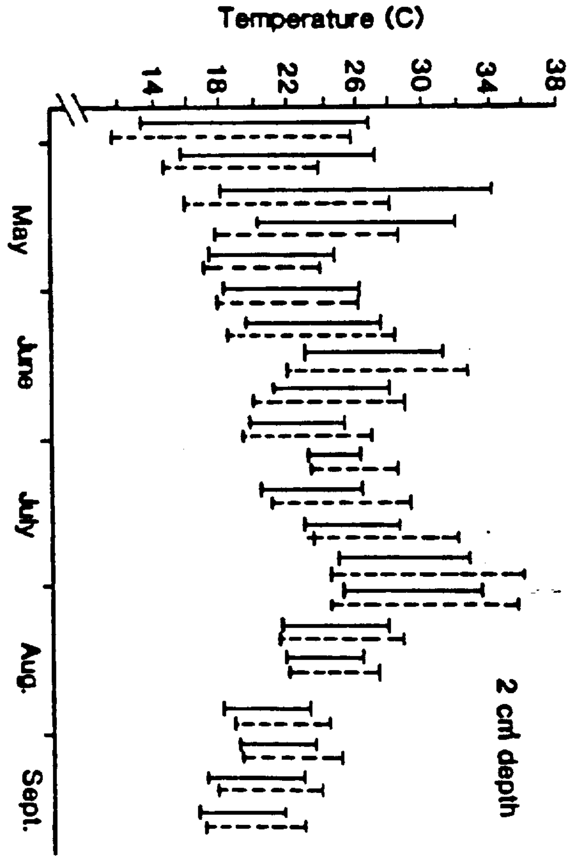
1. Summarized from Greegor (1986). Future instrumentation descriptions are in NASA (1988).



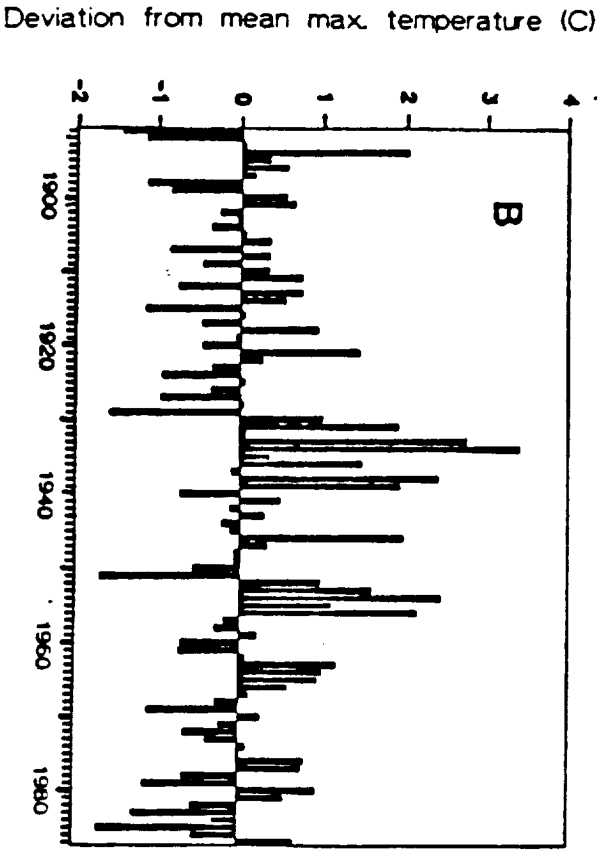
ANNUALLY BURNED
UNBURNED
600
400
200
1975
76
77
78
79
80
81
82
83
84
85
86
YEAR

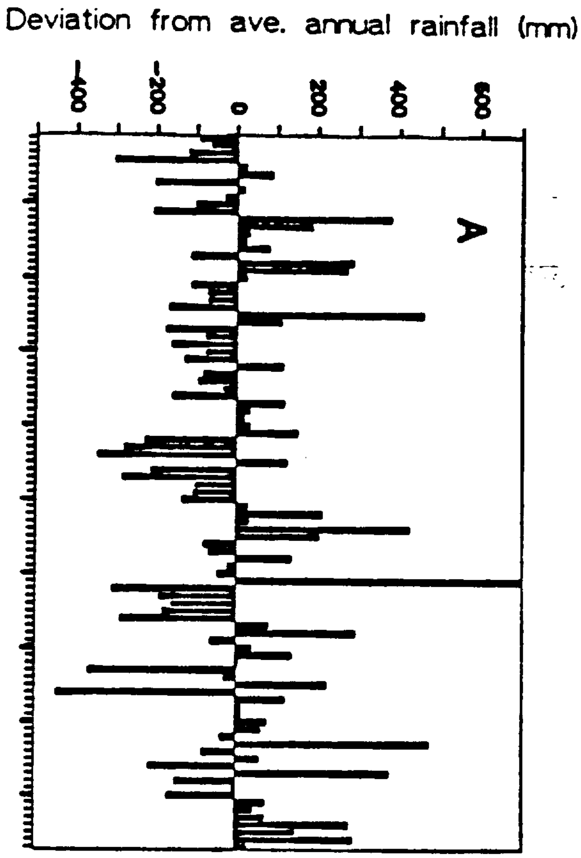


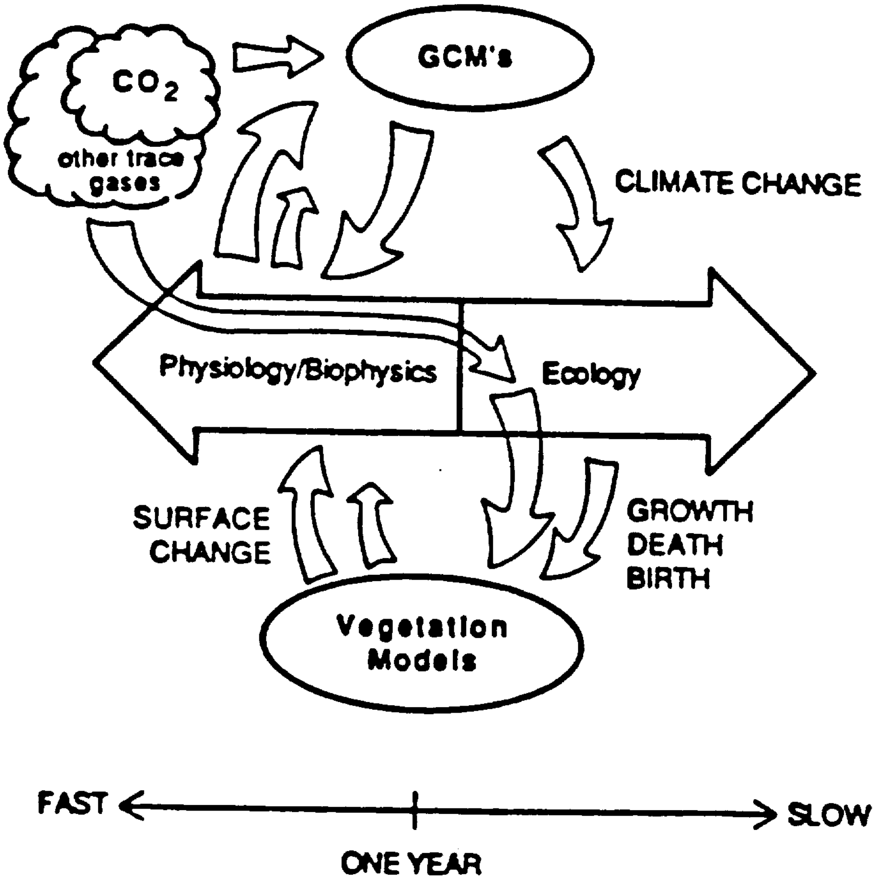
Temperature (C)
14
18
22
26
30
34
May
June
July
Aug.
Sept.
10 cm depth

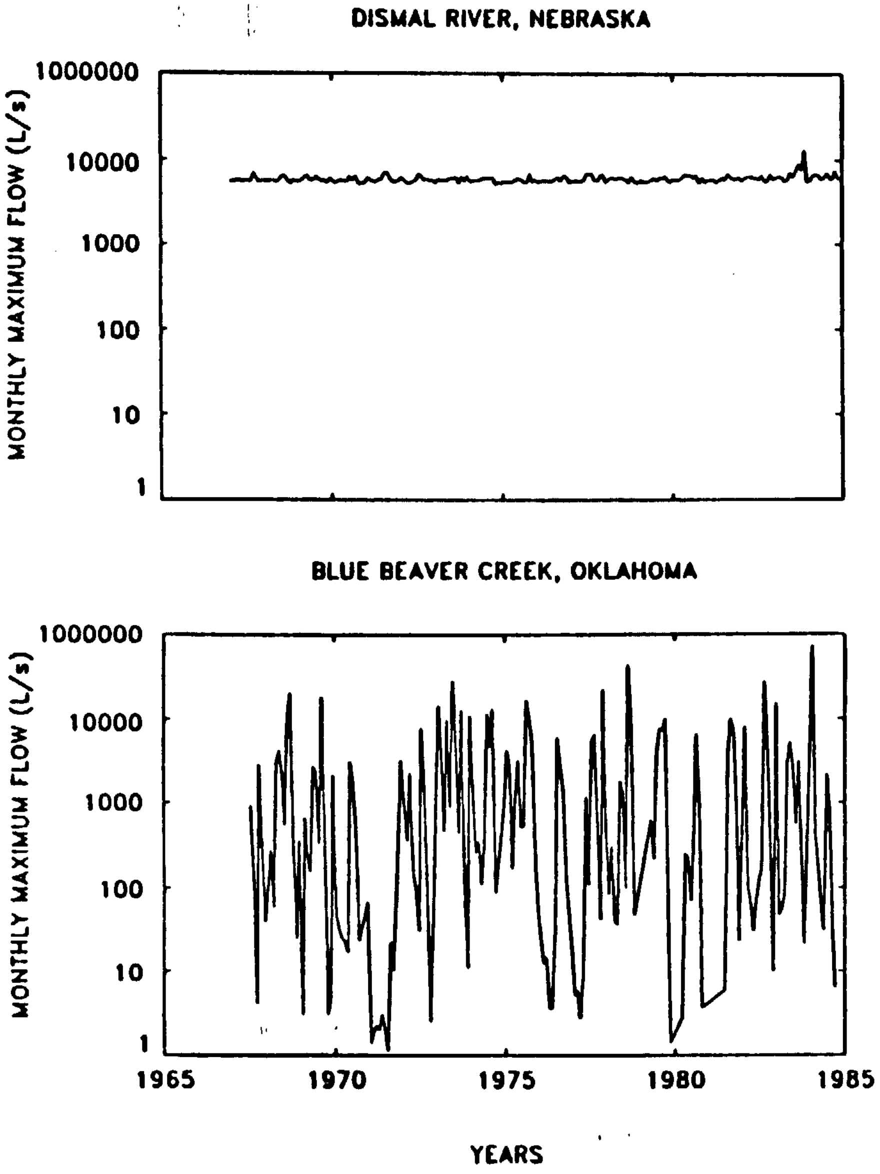


Temperature (C)
14
18
22
26
30
34
38
May
June
July
Aug.
Sept.
2 cm depth


Deviation from mean max. temperature (C)
B
-2
-1
0
1
2
3
4
1900
1920
1940
1960
1980


Deviation from ave. annual rainfall (mm)
A
-400
-200
0
200
400
600


CO$_2$
other trace gases
GCM's
CLIMATE CHANGE
Physiology/Biophysics
Ecology
SURFACE CHANGE
GROWTH
DEATH
BIRTH
Vegetation Models
FAST
SLOW
ONE YEAR


DISMAL RIVER, NEBRASKA
MONTHLY MAXIMUM FLOW (L/s)
1000000
10000
1000
100
10
1
BLUE BEAVER CREEK, OKLAHOMA
MONTHLY MAXIMUM FLOW (L/s)
1000000
10000
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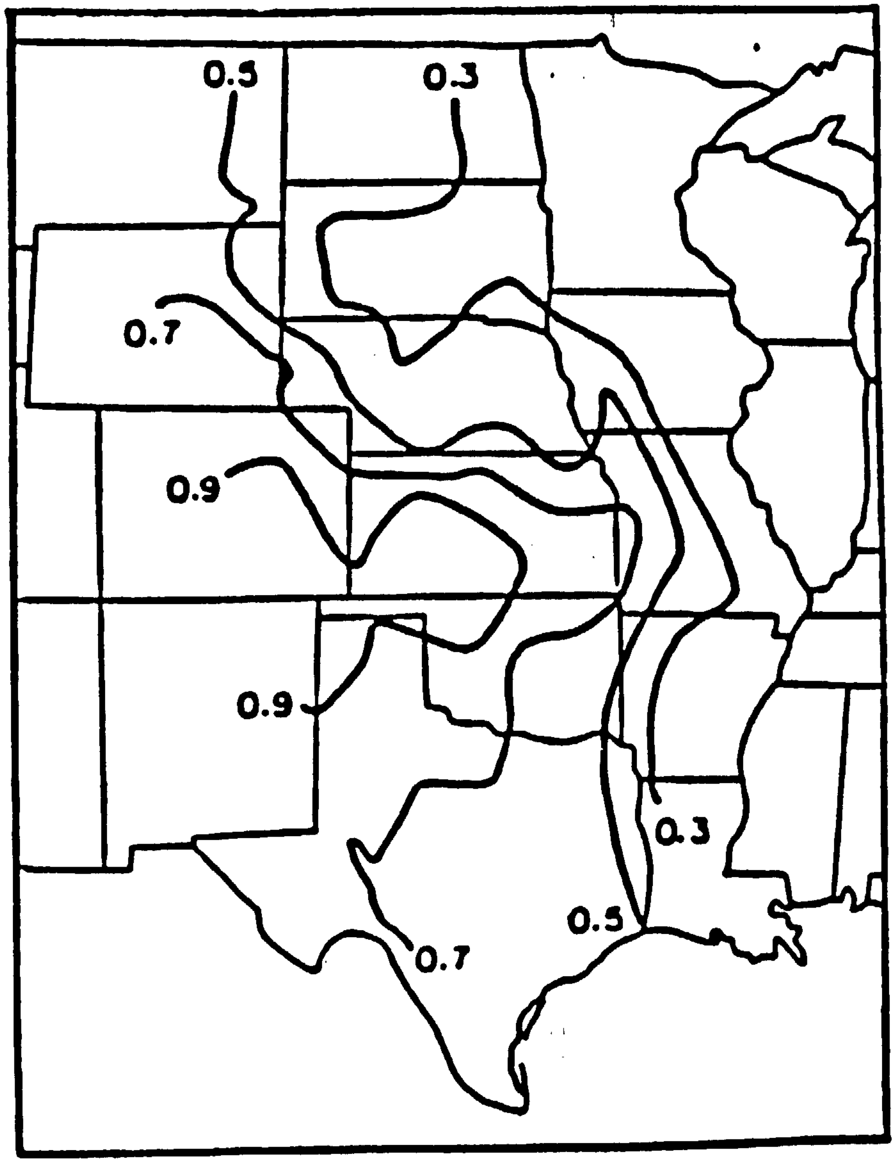
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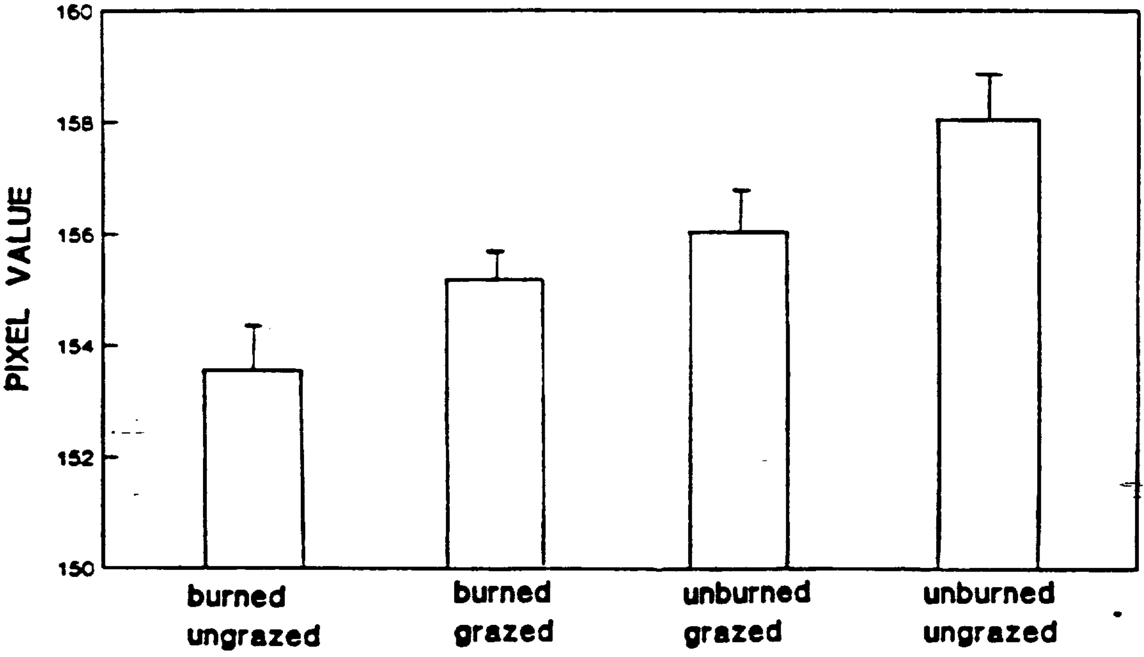

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Ecology, 72(2), 1991, pp. 672–684
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PHYSIOLOGICAL INTERACTIONS ALONG RESOURCE GRADIENTS IN A TALLGRASS PRAIRIE[1]

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Abstract. Spatial variability in availability of resources that limit photosynthesis (water and N) leads to variation in rates of atmosphere–biosphere exchange. N content and allocation are canopy properties that link ecosystem, physiological, and biophysical processes and that vary in space at scales relevant to atmosphere–biosphere interaction. We studied landscape-scale variation in these and related canopy properties in Kansas Tallgrass Prairie (USA). The tallgrass ecosystem was suited to this investigation because primary production in the prairie is constrained by N availability. This work was designed to aid in interpretation and spatial extrapolation of gas exchange measurements made using aerodynamic techniques as part of FIFE (First ISLSCP Field Experiment), a NASA-supported study. We collected data on spatial distribution of biomass, leaf area index (LAI), canopy N mass, N concentration ([N]), and gas exchange along topographic and management gradients. We also measured height distribution of N, light interception, and gas exchange within canopies as a function of position in the landscape. Substantial variation in biomass, LAI, N accumulation, and N allocation occurred over time, with topography, and as a result of previous burning. The vertical gradient of [N] and photosynthetic capacity within canopies were correlated, in space and time, with biomass and canopy light interception. The gradients were steeper in high biomass sites than in low biomass sites. In addition, proportional N allocation to the upper layer increased with time (12% in June, 32% in August) as biomass increased. As nutrient uptake increased within the tallgrass landscape, biomass increased and light limitation in the lower canopy was induced. As this light limitation increased with increasing biomass, or with accumulation of dead vegetation, allocation of N to the upper canopy increased. Height distribution of photosynthetic capacity paralleled within-canopy N allocation and light interception. As resource ratios (light, water, and nitrogen) varied in the landscape, so did rates of gas exchange. This work suggests that interactions between light extinction, N allocation, and photosynthesis that have been proposed for monospecific stands apply to the multispecies, but structurally simple, canopy of the tallgrass prairie. Models of plant performance based on evolutionary arguments may provide a powerful basis for spatial extrapolation of atmosphere–ecosystem exchange rates from sites to landscapes and larger regions.

Key words: atmosphere–ecosystem exchange; FIFE; fire; Konza Prairie Long-Term Ecological Research site; leaf area index; light interception; nitrogen allocation; photosynthetic capacity; photosynthetically active radiation; remote sensing; toposequences.

INTRODUCTION

Spatial variability in limiting resources for plant growth leads to variation in rates of atmosphere–biosphere exchange of water and carbon dioxide. Current models of biophysical interaction at the land surface generally employ simple representations of vegetation, in which the behavior of the vegetation is assumed to be controlled by temperature, precipitation, and soil hydraulic properties. Ecosystem and physiological models include additional controls over primary production and gas exchange, such as nutrient availability and herbivory. Ecosystem and physiological modelers have consistently identified nutrients to be important regulators of productivity (Aber et al. 1978, Ingestad and Lund 1986, Pastor and Post 1986, Hirose and Werger 1987*a*, *b*, Parton et al. 1987). Because nutrient availability varies at landscape, regional, and global scales, inclusion of nutrient constraints is critical for the correct representation of spatial variability in rates

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[1] Manuscript received 26 June 1989; revised 10 April 1990; accepted 30 May 1990.

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of atmosphere–ecosystem exchange. In contrast, current biophysical models (Eagleson and Segarra 1985, Sellers et al. 1986, Wilson et al. 1987) ignore nutrient control.

Many of the differences in approach between ecosystem and biophysical models originate in the multiple temporal and spatial scales at which gas exchange and primary productivity are controlled (Jarvis and McNaughton 1986). Schulze (1986) observed that "the exchange of carbon dioxide and water vapor between plants and the atmosphere is regulated in the long term (days to weeks) by changes in leaf area and by the development of a photosynthetic apparatus in the leaf mesophyll, and in the short term (hours to days) by the adjustment of photosynthetic capacity and changes in stomatal aperture." Schulze's "long-term" changes are constrained by soil resource availability, which varies strongly in space. Research on atmosphere–biosphere coupling and climate change requires consideration of short-term biophysical interactions over longer time scales of change in the plant/soil system (Gates 1985, Bolin 1988).

Increasing the biological sophistication of models of atmosphere–ecosystem interactions requires the development of techniques for relating key ecological/physiological responses to environmental drivers. Mooney and colleagues have argued that for a given environmental problem there exists a limited array of physiological and morphological solutions (convergent evolution: Mooney 1977, Orians and Solbrig 1977). If this is often the case, it suggests that quantitative "rules" about plant response to environmental conditions of water, nutrients, etc. may have broad application (i.e., Thornley 1972). In a key application for atmosphere–biosphere interactions, Field (1983) suggested that N allocation should be driven by light extinction within canopies to maximize carbon gain per unit N as a consequence of selective pressures shaping plant attributes. This "rule" describing N allocation within canopies has generally been found to apply in laboratory studies (Hirose and Werger 1987*a*) and monospecific stands in the field (Hirose and Werger 1987*b*, Hirose et al. 1988). The predictive ability of this model has not been tested in the field along gradients of resource availability. If the allocation of N varies with height within mixed-species canopies, as expected from studies of monospecific stands, this provides a useful new tool for spatial extrapolation of canopy-exchange models, since N allocation influences canopy photosynthesis.

This research was conducted as part of the FIFE project (First ISLSCP Field Experiment, ISLSCP = International Satellite Land Surface Climatology Project). FIFE included ground and aircraft measurements of biophysical fluxes and coordinated satellite and aircraft remote-sensing observations (Sellers et al. 1988). FIFE included ground-based eddy correlation measurements of CO_2 exchange, which were limited in their spatial coverage of the landscape because there were fewer systems available than landscape positions and because their terrain requirements precluded their use in steep areas and narrow valleys (Verma et al. 1990). Aircraft eddy correlation measurements were spatially extensive, but had coarse spatial resolution (≈ 1 km) relative to topographic variation (Desjardins et al. 1990). Our study was designed, in part, to form the basis for extrapolation of point gas-exchange measurements to the region by linking mappable terrain and management units to plant properties thought to regulate gas exchange (Davis et al. 1990, F. W. Davis, *unpublished manuscript*). A scheme to extrapolate point measurements of gas exchange based on landscape–plant relationships presented in this paper is reported by F. W. Davis (*unpublished manuscript*).

The objectives of this study were (1) to analyze spatial and temporal variability in slowly changing controls over gas exchange and to relate them to canopy fluxes of water and CO_2 as determined by other FIFE investigators, (2) to identify links between biological processes and remotely measurable canopy parameters for the use of remote sensing to obtain data on spatial variability in ecosystem properties, and (3) to test whether a model of allocation based on evolutionary arguments for single plants applies to mixed communities along gradients of limiting factors.

METHODS

This research was conducted in Kansas Tallgrass Prairie, largely at the Konza Prairie Research Natural Area (KPRNA) and adjacent Kansas State University property used for grazing research. The Konza Prairie is located in the Flint Hills region of eastern Kansas, USA, ≈ 10 km south of Manhattan, Kansas. The KPRNA is a 3487-ha area of native tallgrass prairie with vegetation dominated by the grasses *Andropogon gerardii* Vit., *Sorghastrum nutans* (Michx.) Nash, and *Panicum virgatum* L. The Flint Hills are steep and rocky and are unsuitable for conventional farming; the region is used primarily for cattle production (Launchbaugh and Owensby 1978). Flint Hills bedrock is composed of alternating layers of shale and limestone, leading to a "stair-step" appearance with steep slopes and shallow soils forming over limestone and shallow slopes with deep soils over shale (Fig. 1). Occasional loess deposits are found on ridgetops. The region has a continental climate with 835 mm mean annual precipitation, $-2.7°C$ mean January temperature, and $26.6°C$ mean July temperature (Bark 1987). The KPRNA is a National Science Foundation Long-Term Ecological Research site. The research program has included controlled burning since 1972.

Landscape sampling

We measured a series of plant properties and processes along east-west transects that spanned ungrazed watersheds, beginning and ending on uplands (Fig. 2A,

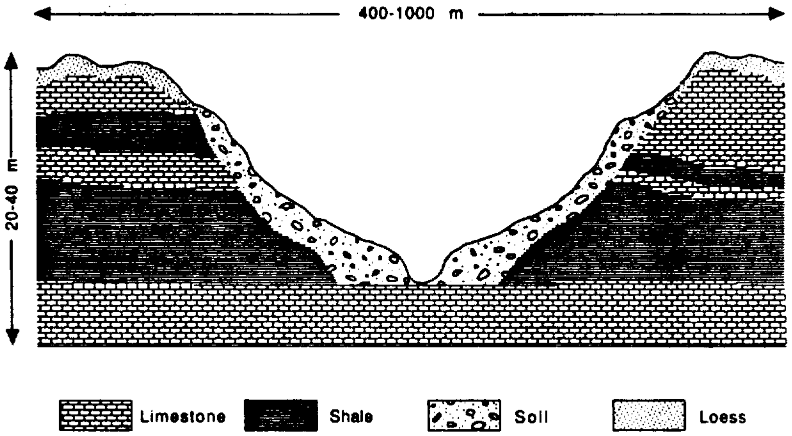


FIG. 1. An idealized cross section through a Konza watershed. Soil depth increases downslope, but incision to bedrock may occur in the ephemeral channel. Loess caps may occur on ridgetops as shown, although not all ridgetops have such deposits. Transects used in this study spanned four such toposequences; physiological studies were carried out in lowland positions, usually just above the drainage channels, and on steep limestone sites at slope shoulders.

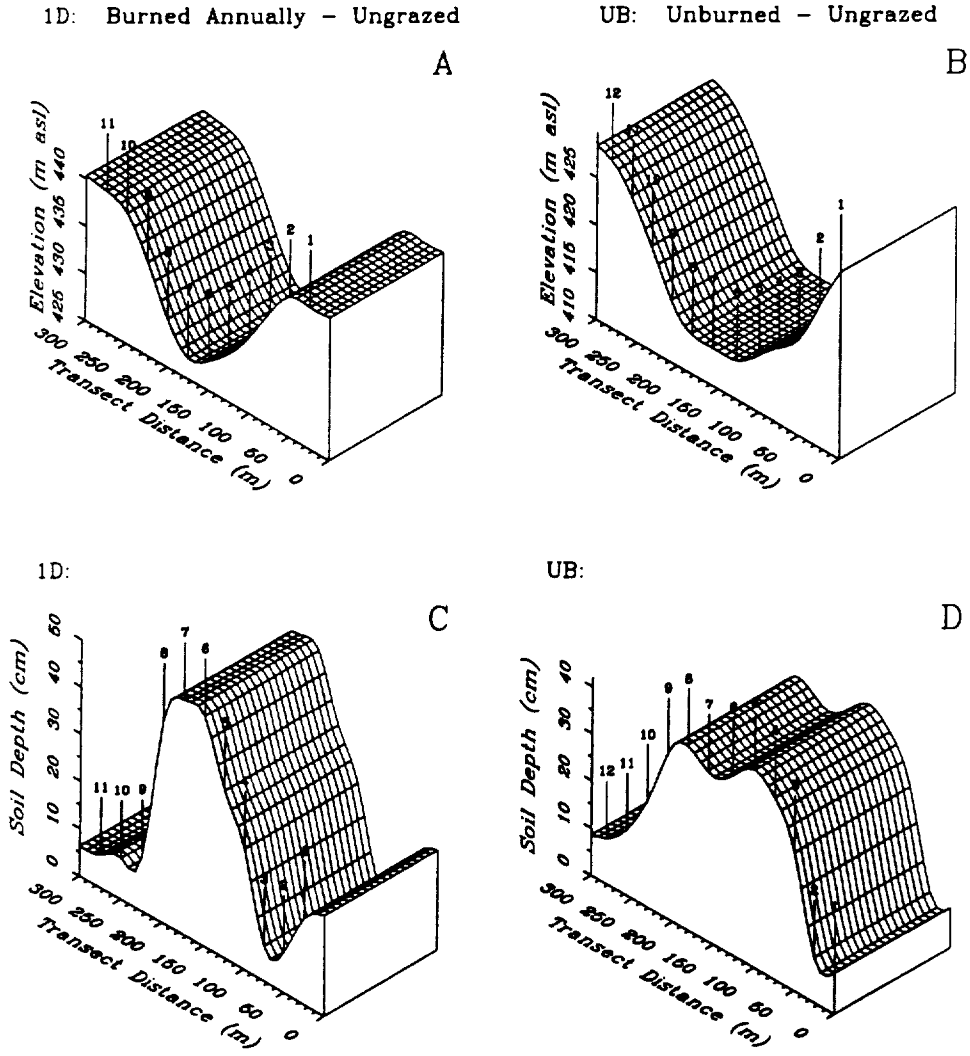
B). Measurements were made at 25-m intervals along transects that varied in length from 275 to 400 m. Transects were studied in two annually or biennially burned and two unburned, ungrazed watersheds to capture the effects of management. At each sample point, three 0.1-m^2 plots were chosen at random distances normal to the transect, i.e., along the contour. All aboveground live and dead plant material was harvested from each plot. Soil depth was measured at each plot using a T-handled probe, pushed into the soil to bedrock contact. Maximum measurable depth was 50 cm. Slopes between sample points along the transect were measured using a Brunton compass. Harvested plant material was separated into live grass, dead grass, and total nongrass portions. Each fraction was dried to constant mass and analyzed for total nitrogen (Nelson and Sommers 1980, Schimel et al. 1985). Leaf area index (LAI) was computed for each sample using LAI–biomass regressions developed from independent sampling by FIFE staff scientists, using separate models for burned and unburned vegetation at each date (Table 1). Some evidence suggested that LAI values used may have been low due to leaf curling, but there was no evidence of bias as a function of landscape position or treatment (B. Blad, *personal communication*). Transects were sampled in late May, late June, mid-August, and mid-October 1987 coincident with FIFE intensive field campaigns (IFCs) (Sellers et al. 1988). Canopy nitrogen variables included [N] (in milligrams per gram), N mass per unit sample area (in kilograms per hectare), and N per unit leaf area (grams per square metre leaf area). We will refer to N mass per unit sample area as "N mass."

Root N was sampled along a burned and an unburned watershed transect in 1989. Cores were taken to 30 cm or bedrock contact. We did not attempt to recover all root biomass but instead collected sufficient live root material to obtain an estimate of live root [N] from each core. Live roots were identified visually based on color and texture. Each sample was a composite of three or more cores so as to obtain sufficient material for analysis. Root material was then analyzed for N content.

We fit nonlinear surfaces to the biomass, N, and LAI data. Transect location and time of year served for x and y coordinates, respectively, and the various plant parameters as z. Data were interpolated using a kriging algorithm and surfaces were estimated using a cubic spline (Surfer, Golden Graphics, Golden, Colorado).

Canopy sampling

We studied canopy structure by analyzing light, canopy mass, and nitrogen content as a function of height (Hirose et al. 1988). Replicate plots (4–5) were sampled in late July 1988 and 1989 from maximum and minimum biomass locations on selected transects based on 1987 biomass data. Plots were located at random distances normal to transects as for landscape sampling. A frame was constructed with dimensions 1 m height by 0.1 m^2 area. A moveable quadrat within this frame allowed us to sample the vegetation above a chosen height in 10-cm vertical increments. We determined canopy height and then divided the canopy vertically into layers, usually thirds, for sampling of light, biomass, and N. At a few unproductive sites, the canopy could only be divided in half. Photosynthetically active radiation (PAR) was measured at the top of the canopy, at sampling heights within the canopy, and beneath the canopy using a 1-m line quantum sensor (LI-COR, Lincoln, Nebraska). Intercepted PAR (IPAR) was calculated as the ratio of PAR beneath the canopy, or a portion of the canopy, to incoming PAR. Vegetation was harvested at the sampling heights working downward. Biomass and [N] were determined



1D: Burned Annually – Ungrazed

UB: Unburned – Ungrazed

1D:

UB:

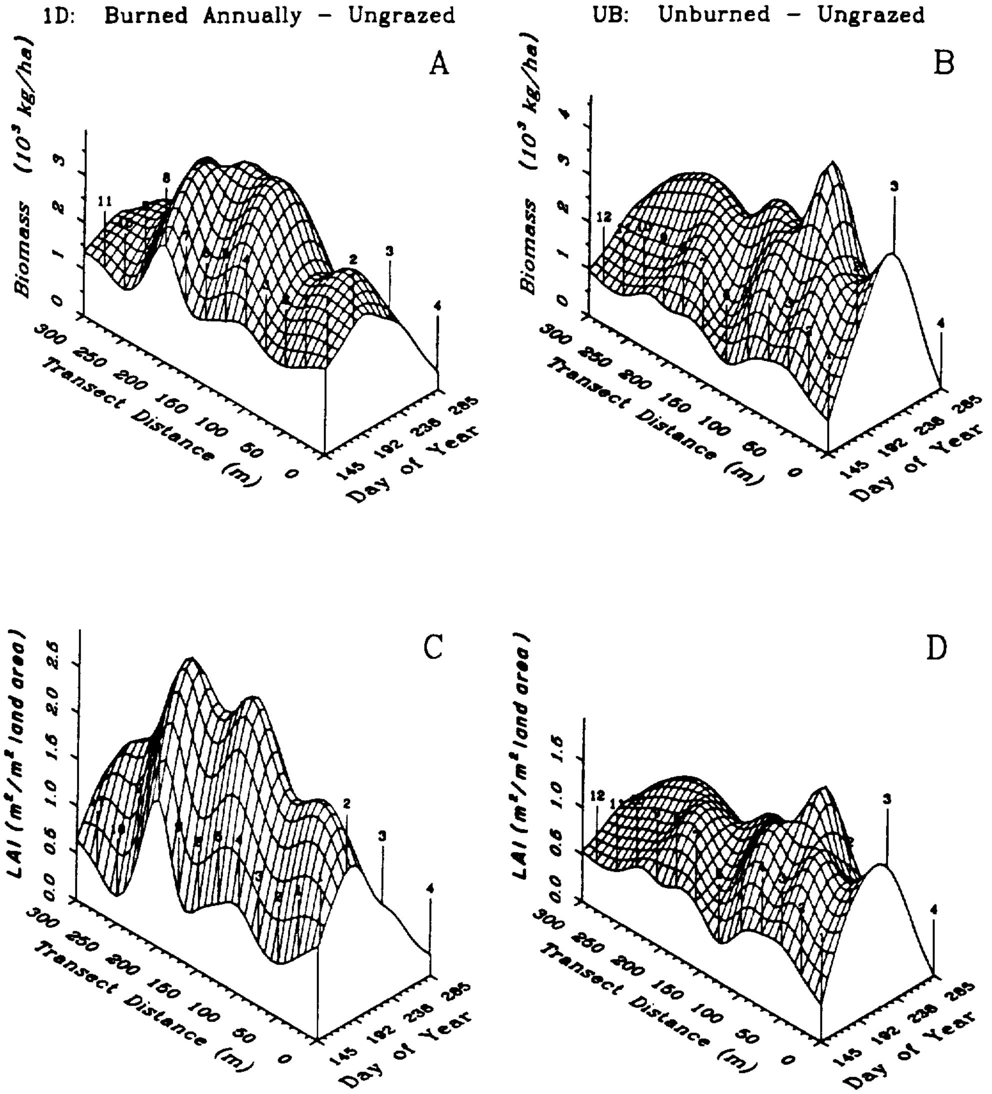
FIG. 2. Landscape data for two selected transects. Sample points are indicated by numbered posts. The full experiment sampled four ungrazed watersheds. (A) and (B) Elevation transects, showing topography of burned and unburned study sites, respectively. asl = above sea level. (C) and (D) Soil depths across the same transects. Note the vertical exaggeration.

for each vertical increment. PAR measurements were not integrated over time, but replicate plots within biomass categories were sampled at different times of day between 0949 and 1627 Central Daylight Time.

We also sampled the height distribution of N in canopies on two dates (June and August 1987) at a burned high biomass site to determine N allocation responses over time. Eight replicate plots were sampled. Biomass accumulation at the site chosen for this time course study was 5730 kg/ha.

Gas-exchange methods

We measured photosynthetic capacity and the light response of photosynthesis as a function of height within the canopy and landscape position in 1989. We chose sites for photosynthesis measurements using criteria similar to those used for the light interception studies, choosing areas of minimum and maximum biomass in two watersheds. We measured CO_2 uptake with a field-portable, closed flow gas-exchange system (LI-COR model 6200). Leaves were exposed to ambient conditions inside and outside the cuvette, except for PAR manipulations. Leaves were sealed in the cuvette for no more than 25 s; CO_2 was depleted by no more than 5 μL/L during measurements. Humidity and vapor pressure deficits were maintained at ambient levels by adjusting the portion of gas that flowed through a desiccant. Light response curves were obtained by reducing ambient PAR on cloudless days using stacked neutral density screens. Light response curves were fit using the equation for a nonrectangular hyperbola (Johnson and Thornley 1984). Photosynthetic capacity was determined as CO_2 uptake (micromoles per square metre per second) at full sunlight. Photosynthetic ca-



1D: Burned Annually – Ungrazed

UB: Unburned – Ungrazed

FIG. 3. Biomass and leaf area index (LAI) data from transects shown in Fig. 2. Surfaces are plotted as a function of transect distance and time (the four IFCs in 1987). Sample points and IFC dates are indicated by numbered posts. (A) and (B) Live aboveground biomass for burned and unburned transects, respectively. (C) and (D) LAI across the same transects. LAI was computed using equations from Table 1.

pacity for lower canopy layers was determined by allowing exposure to full sunlight. In general, 3–4 leaves were placed in the cuvette. Two or more independent replicate measurements were made at each site. In some cases, logistics permitted sampling replicates of landscape position (e.g., two lowland sites per watershed) while, in other cases, intermittent cloudiness only permitted one replicate of landscape position per watershed.

RESULTS

Landscape pattern

Our data indicate that there are large variations in constraints on atmosphere–ecosystem exchange with topography and burning management (Figs. 2–4). Aboveground biomass accumulation (Fig. 3A, B) varied strongly as a function of position in the landscape (Fig. 2A, B). Biomass increased downslope with increasing soil depth in both burned and unburned landscapes (Fig. 2C, D). Very shallow soil depths found at the top of slopes likely result in both water and nitrogen constraints on growth. Valley bottoms had deep soils, but highly variable biomass because of disturbance associated with ephemeral stream channels; because of this, correlations between soil depth and biomass were significant but not strong ($r^2 = 0.12$, $P < .06$ to $r^2 = 0.35$, $P < .001$ for different watersheds). Biomass time series varied as a function of management: burned sites accumulated greater biomass earlier (Fig. 3A, B, Table 2).

Leaf area dynamics were different in burned and unburned watersheds. Leaf area in burned areas at-

TABLE 1. Coefficients and statistics for leaf area index (LAI): biomass conversion equations. Insignificant green biomass occurred during IFC 4. The regression equations have the form LAI (in m²/m²) = Intercept + (Slope) × (live biomass, in kg/ha). *n* = sample size.

Date*	Intercept	Slope	r^2	*P*	*n*†
		Burned sites			
IFC 1	−0.64	0.0009	0.74	<.001	36
IFC 2	0.49	0.0007	0.86	<.001	54
IFC 3	0.03	0.0004	0.67	<.001	36
		Unburned sites			
IFC 1	0.02	0.0006	0.52	<.001	96
IFC 2	0.14	0.0005	0.72	<.001	144
IFC 3	0.04	0.0004	0.60	<.001	96

* Dates for Intensive Field Campaign (IFC) 1: 26 May–6 Jun 1987, IFC 2: 25 Jun–15 Jul 1987, IFC 3: 10 Aug–21 Aug 1987.

† Variable sample sizes result from the number of sample dates that fell within a period commencing 1 wk prior to and concluding 1 wk following each IFC.

tained much higher values and tended to peak earlier than in unburned sites (Fig. 3C, D, Table 2). The difference in temporal amplitude in LAI between burned and unburned sites is exaggerated compared to that for biomass (Fig. 3, Table 2). This is due to lower specific mass (mass per unit leaf area) in burned sites than in unburned sites, as is apparent from comparison of LAI–biomass regression slopes (Table 1). Differences in LAI–biomass relationships may result from differences in physiology and from changes in species composition with burning (Towne and Owensby 1984).

Variations in canopy N mass (Fig. 4A, B, Table 3) reflect levels of net N mineralization since virtually all inorganic N mineralized in tallgrass prairie soils is taken up by vegetation (Ojima 1987, Seastedt and Hayes 1988). Export in soil solution or as gases is negligible (Seastedt and Hayes 1988, D. S. Schimel and A. R. Mosier, *personal observation*). Consequently, we expect lower canopy N mass to occur where N availability is lower, rather than because of inhibition of uptake by some other limiting factor (i.e., water). Differences in canopy N mass could also reflect changes in N allocation between roots and aboveground organs. Our other studies suggest that such changes are small relative to the differences in canopy N mass observed (Ojima 1987). Based on these assumptions, it appears that large variations in soil N availability occurred with position within the landscape.

Spatially, canopy N mass was generally correlated with biomass, with higher amounts in toeslope or lowland areas (Fig. 4A, B). Temporal patterns varied notably with landscape position and strongly with burning management. As with biomass, N uptake into the canopy in unburned systems lagged behind that in burned systems and was lower overall. N concentration per unit mass (Table 2) or per unit leaf area (Fig. 4C, D) was generally higher in unburned than burned sites and declined with time in both.

Data on plant water stress (xylem pressure potential) collected along topographic sequences in 1989 showed that minimum water stress occurred where N availability appeared to be highest (i.e., in lowland sites: A. K. Knapp and D. S. Schimel, *personal observation*). The correlation of water and N availability within the landscape means that either factor may be that which most limits productivity, depending upon their relative abundance over time.

Root N concentrations varied within landscapes: upland sites had higher N concentrations than lowland sites (Fig. 5A, B). The separation into upland and lowland sites was based on data shown in Fig. 2, with lowland sites taken as sites with soil depth >20 cm. No differences were apparent between the burned and unburned watersheds, but no replication exists for this contrast. N concentration at upland sites averaged 3.3 ± 1.3 mg/g (mean ± 1 SE) in burned and unburned sites alike, while lowland sites averaged 2.6 ± 1.7 and 2.2 ± 1.4 mg/g in burned and unburned sites, respectively.

Canopy structure

Although net primary production is generally N limited in tallgrass prairie sites, photosynthesis may become light limited in productive areas. As biomass

TABLE 2. Summary of plant parameters by treatment and date, averaged over replicates and landscape position. Treatments are blocked by burned (annually or biennially) vs. long-term unburned (through 1987).

	Plant parameters*					
	Biomass (kg/ha)		[N] (mg/g)		LAI (m²/m²)	
Date	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
			Burned sites			
Transect 1D†						
IFC 1	1610	520	13.5	1.8	0.8	0.5
IFC 2	2800	1050	8.8	2.3	2.4	0.7
IFC 3	3160	920	6.7	1.0	1.3	0.4
Transect 2D						
IFC 1	1540	460	12.1	1.6	0.7	0.4
IFC 2	2450	880	8.4	0.9	2.2	0.6
IFC 3	1580	410	7.2	1.1	0.7	0.2
			Unburned sites			
Transect UB						
IFC 1	1040	370	18.1	2.2	0.6	0.2
IFC 2	2050	1020	10.3	1.4	1.2	0.5
IFC 3	3260	1230	8.6	1.3	1.3	0.5
Transect N4						
IFC 1	800	370	15.0	2.3	0.5	0.2
IFC 2	1450	870	10.3	1.9	0.9	0.4
IFC 3	1290	590	9.2	1.7	0.6	0.2

* Biomass and [N] are for aboveground live grass material. LAI values were calculated according to equations in Table 1. Only trace amounts of live biomass occurred at IFC 4.

† Transect identifiers denote research watersheds of the Konza Prairie Long Term Ecological Research site; for detailed information, contact the Data Manager, LTER, Division of Biology, Kansas State University.

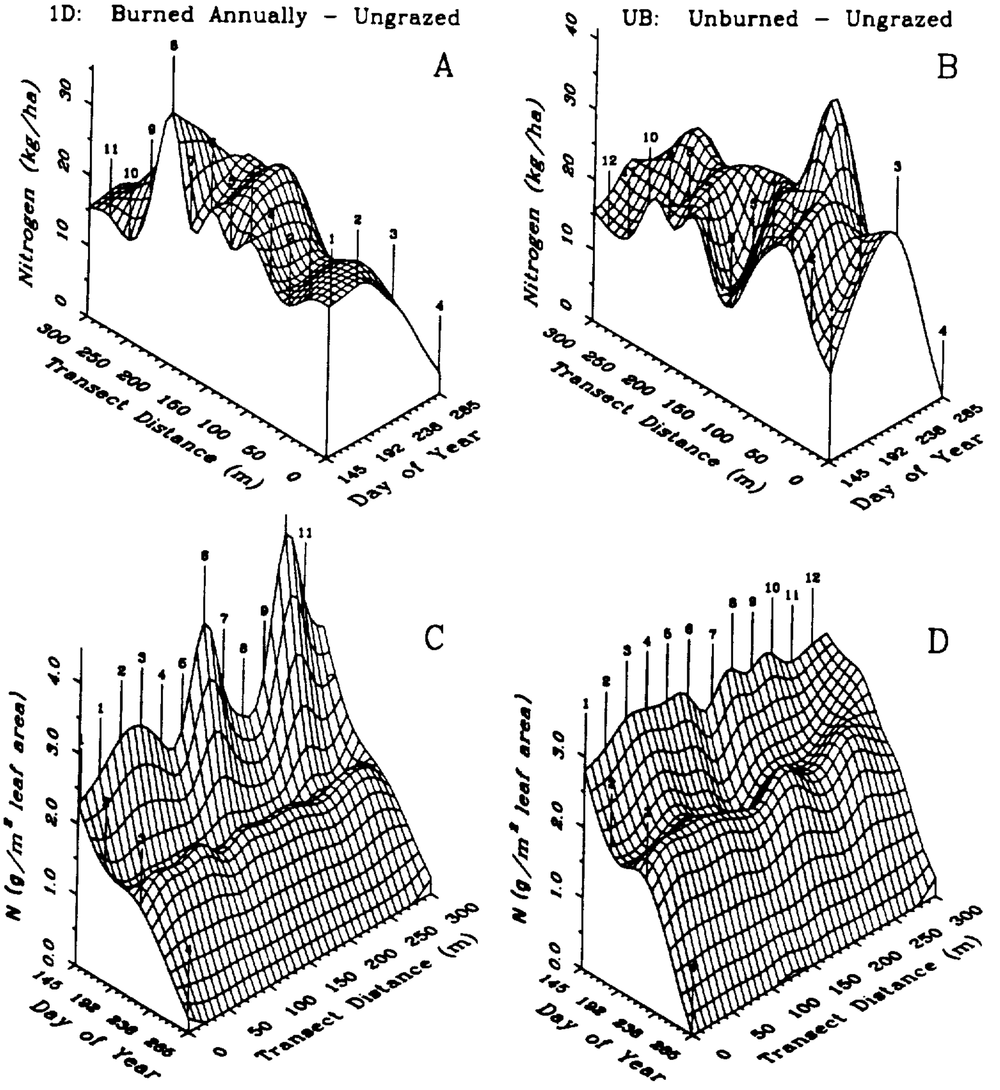


FIG. 4. N data from transects shown in Fig. 2, plotted against transect distance and time as in Fig. 3. (A) and (B) N mass in live vegetation, per unit sample area. (C) and (D) N per unit leaf area (N mass per unit sample area LAI), a correlate of maximum photosynthetic rate. There was no live biomass at IFC 4. Note that (C) and (D) were rotated to best display dynamics.

increases, self-shading should also increase, as is evident from the comparison of canopy IPAR between high and low biomass sites in Table 4. When N concentrations for high and low biomass light interception sites were compared, the gradient of [N] with height ($[N]_t/[N]_b$, where $[N]_t$ is [N] in the top canopy layer and $[N]_b$ is [N] in the bottom layer) was steeper in high biomass sites than low biomass sites and was correlated with total IPAR (Fig. 6). This is in accordance with the hypotheses of Hirose and Werger (1987*a*), based on a theory of N allocation to maximize carbon gain.

The data suggest that as light limitation (self-shading) increased with increasing biomass or litter, the plants responded by increasing the allocation of N to the upper canopy. A time sequence of N distribution with height is shown in Fig. 7A and B. As canopy mass increased through the growing season, proportionately more N was allocated to the upper layers. In June, only 12% of canopy N was found in the top layer of the canopy, compared with 32% in August (Fig. 7A). Hirose et al. (1988) showed that the changing light environment with depth in canopies drives N allocation subject to constraints imposed by leaf age.

Plants in long-term unburned high biomass sites had the steepest gradients of [N] (watershed UB), with highest upper canopy layer leaf $[N]_t$ and light extinction (percent $IPAR_t$) (Fig. 8, Table 4). This suggests that plants compensated for additional shading from accumulated dead biomass by shifting photosynthetic apparatus into the upper canopy. Despite this adjustment,

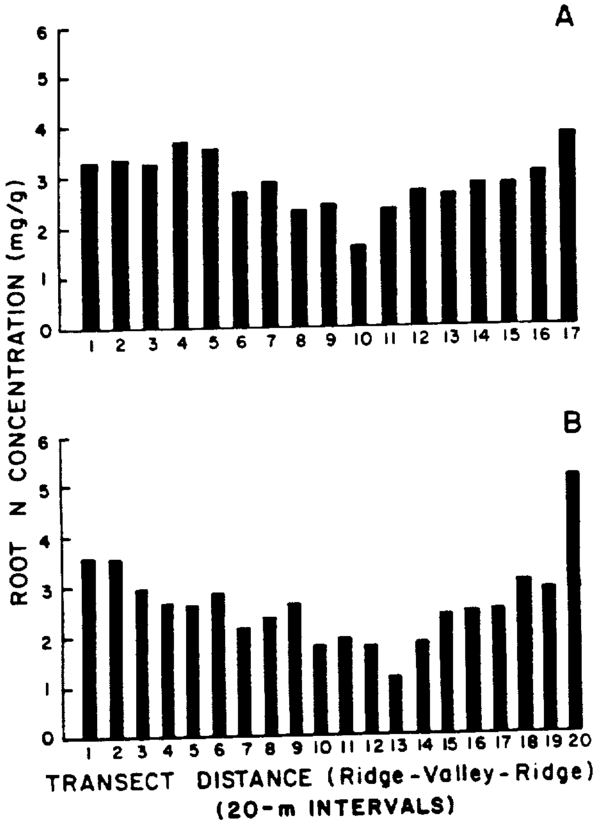


FIG. 5. Root [N] along (A) transect 1D—annually burned, and (B) transect UB—unburned. Samples were collected in 1989. Data shown are from composited cores collected 20 m apart. For transect topography refer to Fig. 2A and B, respectively.

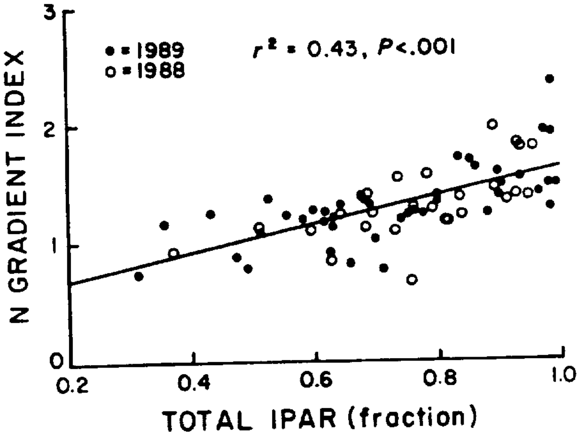


FIG. 6. The N gradient index ([N] in the top canopy layer/[N] in the bottom canopy layer) plotted against total IPAR (expressed as fraction of incoming PAR) for 1988 and 1989. As IPAR increased, the gradient in N allocation within the canopy became steeper.

other studies have shown burned sites to be substantially more productive than unburned in most years, with much of the difference appearing in the root mass (Towne and Owensby 1984, Ojima 1987). While canopy IPAR was not higher in unburned than burned high biomass sites, dead plant material must have intercepted some PAR (Table 4). Knapp (1984) demonstrated reductions of as much as 58.8% in available light in unburned canopies.

The response of the plants to self-shading is further illustrated by considering the relationship between total biomass and [N] of the top canopy layer (Fig. 8A, B). As live-plus-dead plant material increased, [N] in the top layer ($[N]_t$) increased. Differences in $[N]_t$ between high and low biomass sites were larger than corresponding canopy [N] differences (Fig. 8, Table 3). The unburned sites had higher $[N]_t$ in both years ($P < .001$, t test). This further demonstrates the effect of shading by dead vegetation on the allocation of N. In unburned sites, the steeper gradient in [N] and higher absolute [N] levels in the top canopy layer had direct effects on stratification of photosynthetic capacity, as is demonstrated below (*Results: Gas exchange*).

TABLE 3. N and biomass within grass canopies of unburned and annually and biennially burned watersheds in 1988. Except where noted, values are for live material. [N] is averaged over the entire canopy.

	Canopy biomass				Canopy N mass (kg/ha)		[N] canopy (mg/g)	
	Live (kg/ha)		Dead* (kg/ha)					
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
			Annually burned					
High biomass	5080	2700			45.5	31	8.4	2.0
Low biomass	1430	350			10.1	2.0	7.1	1.0
			Biennially burned†					
High biomass	2632	196			22.0	3.0	8.3	1.0
Low biomass	1820	294			15.3	3.3	8.3	1.0
			Unburned					
High biomass	2981	1380	999	400	30.1	10.4	10.7	1.0
Low biomass	969	140	243	70	11.8	1.2	12.0	1.0

* Standing dead biomass is shown for the unburned watershed; only trace amounts were found in the burned watersheds.
† The biennially burned watershed was burned in the spring prior to sampling.

TABLE 4. Light interception and canopy height in high- and low-biomass sites from unburned and annually or biennially burned sites in 1988. Total intercepted photosynthetically active radiation (Total IPAR) was calculated as (PAR above the canopy − PAR beneath the canopy). IPAR in the top layer of the canopy (IPAR_t) was calculated as (PAR above the canopy − PAR beneath the top layer). Total IPAR and IPAR_t are reported as percent of PAR above the canopy.

Site type	Canopy height (m)		Total IPAR (%)		IPAR_t (%)		% IPAR_t (100 IPAR_t/ total IPAR)	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
			Annually burned					
High biomass	0.57	0.12	85.5	9.9	17.8	15.0	19.9	15.7
Low biomass	0.34	0.05	38.6	19.5	9.0	9.5	21.9	23.6
			Biennially burned*					
High biomass	0.47	0.11	82.3	7.6	11.8	4.0	14.8	5.2
Low biomass	0.30	0.00	55.0	27.6	23.9	8.2	27.7	16.0
			Unburned					
High biomass	0.57	0.10	83.0	11.3	22.3	9.5	28.4	16.9
Low biomass	0.45	0.06	72.7	6.7	20.2	14.9	27.3	18.8

* The biennially burned watershed was burned in the spring prior to sampling.

Gas exchange

Photosynthetic response paralleled N allocation and light interception within canopies. We calculated the ratio of photosynthetic capacity in the top layer to that found in the lowest layer, in the same manner as for the N gradient index. In 1989, extremely dry conditions resulted in low productivity in burned sites relative to unburned sites, due to higher evaporation in the burned areas, which lacked a litter layer. This climatic anomaly reversed the usual pattern of production found in 1987 and 1988 and as described by Knapp and Seastedt (1986). We compared burned (unproductive) and unburned (productive) lowland sites to analyze the effects of canopy development and light interception on the height distribution of photosynthetic capacity (Fig. 9). In high biomass canopies, marked stratification of photosynthetic capacity occurred with height: capacities in the top layer were on average 3.2 times higher than in the lowest layer. Low biomass canopies exhibited less or no stratification, with a mean ratio of 1.5. Thus, stratification of photosynthetic capacity was stronger than that of [N] (Fig. 6). As found for [N], absolute values of photosynthetic capacity in the top canopy layer were higher in the productive sites than the unproductive sites.

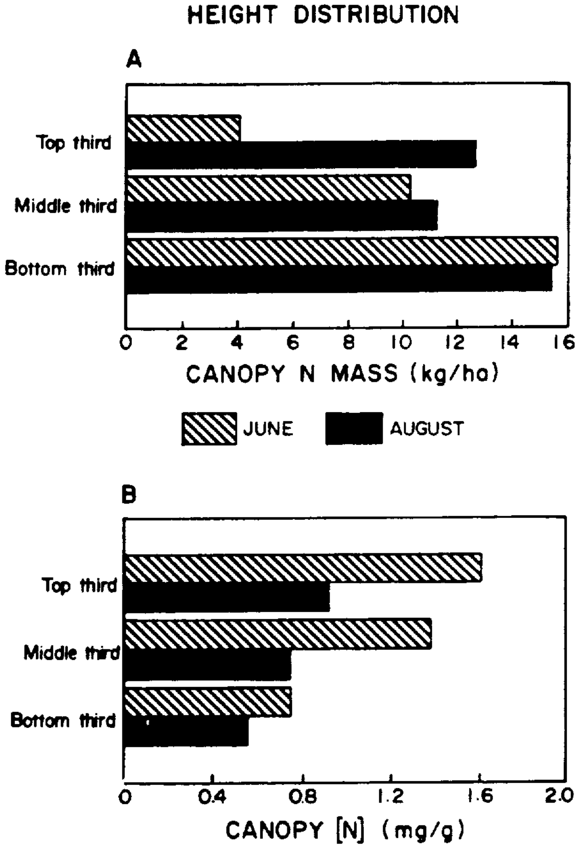


FIG. 7. (A) Nitrogen mass per unit sample area and (B) N concentration as a function of height in the canopy over the growing season. Data are from June and August 1987 sampling of a productive burned upland site. Eight replicate plots were sampled per date.

Light response curves of photosynthesis also varied with canopy height (Table 5, Fig. 10A–C). In all stratified canopies, upper layers had higher maximum rates (Ps_{max}) than lower layers, while the slope at low light (α) increased with height only in the unburned canopy (Table 5). Fig. 10 shows typical stratification of light response curves for burned (Fig. 10A) and unburned (Fig. 10B) prairie grass (*A. gerardii*) from productive sites. These data represent light response under non-water-stressed conditions: the unburned curve (Fig. 10B) was from midseason (July), while the burned data (Fig. 10A) were collected in September after late summer rains had relieved water stress. The lowermost curve (Fig. 10C) shows the response of a nonstratified canopy from an unproductive site; this site may have been somewhat water stressed.

The difference in response between burned and unburned treatments is consistent with trends in N al-

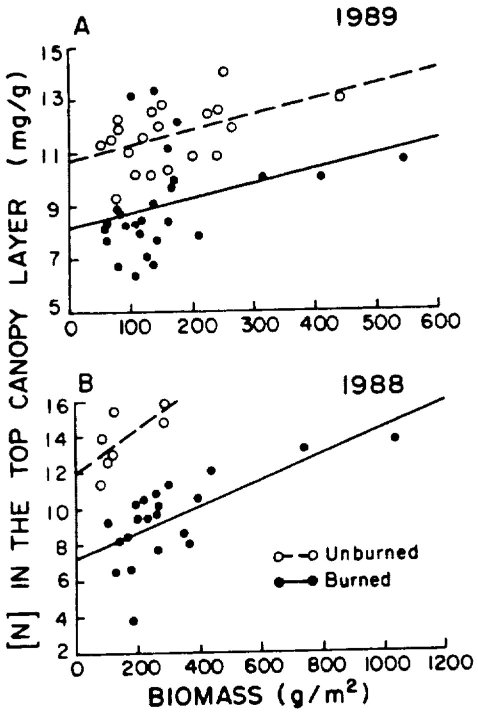


FIG. 8. [N] in the top canopy layer ([N]$_t$) vs. live-plus-dead biomass for (A) July 1989 and (B) July 1988. [N]$_t$ increased as live-plus-dead biomass increased, with generally higher values for the long-term unburned sites. Note difference in scales on both axes in (A) and (B).

location between treatments, supporting the assumption that [N] is correlated with photosynthetic capacity. The burned sites generally had lower N gradient indices and lower absolute N concentrations in the top canopy layer than did unburned sites (Fig. 8). This is consistent with the smaller vertical gradient in photosynthetic capacity found for vegetation on burned vs. unburned sites (Fig. 9). Photosynthetic capacity (Ps_{max}) for a short canopy, with only one measurable layer, was lower than that for upper canopy layers in more productive areas (Fig. 10, Table 5). This is consistent with the trend toward lower [N]$_t$ in short canopies (Fig. 8).

DISCUSSION

Management (burning) and landscape position induced considerable variation in LAI, allocation of N, and gas exchange in the tallgrass prairie ecosystem. Effects of landscape position were via N and water availability (A. K. Knapp and D. S. Schimel, *personal observation*), which appeared to be positively correlated in space. Canopy attributes varied as a function of soil properties and topography, shaped in the long term by soil-forming and geomorphic processes (Pastor et al. 1984, Schimel et al. 1985). The influence of resource availability within the landscape on canopy nutrient allocation and gas exchange was correctly predicted for a multispecies community using a theory based on evolutionary arguments for single plants and previously tested in simple or artificial settings (Field 1983, Hirose et al. 1988).

The use of remote sensing for extrapolation of canopy processes requires that the links between physiological processes, light interception, and spectral reflection be understood. The N allocation results are significant for modeling of photosynthesis from light interception. If photosynthetic capacity is proportional to [N] and if [N] and light extinction have correlated distributions within the canopy, then to a first approximation IPAR and photosynthetic capacity will be linearly related (Field and Mooney 1986, Field 1990, P. J. Sellers, *personal communication*). This is consistent with FIFE results showing linear relationships between spectral vegetation indices, IPAR (Hatfield et al. 1984, Sellers 1985), and CO_2 flux measured using eddy correlation (Desjardins et al. 1990, Hall et al. 1990). The adjustment of photosynthetic capacity in the upper, fully illuminated portion of the canopy to overall light interception allowed IPAR and CO_2 exchange to remain linearly related despite the wide variations observed in IPAR and biomass.

Nitrogen concentration and photosynthetic capacity were not directly proportional within canopies, as the highest value of the N gradient index was ≈1.8, while the ratio of photosynthetic capacity in the upper/lower canopy was as high as 3.2. This suggests that, within the canopy, photosynthetic capacity may be proportional to only that amount of N contained in the photosynthetic apparatus rather than total N. For example, assume a canopy for a productive site with an average [N] of 9 mg/g, an N gradient index of 1.6, [N]$_t$ of 12 mg/g, and 5 mg/g nonphotosynthetic N (a typical total N value at senescence; Hobbs et al., *in press*). The

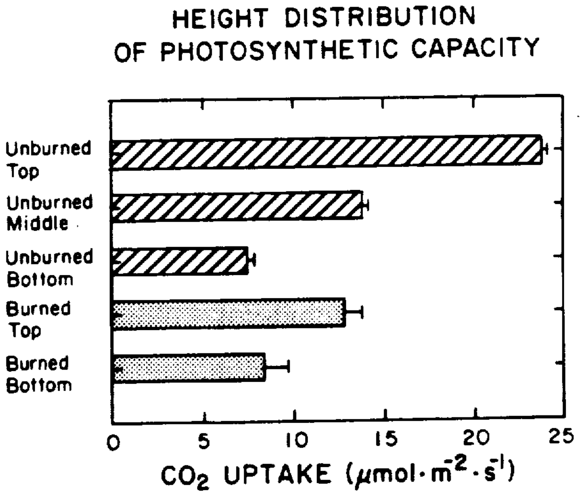


FIG. 9. Photosynthetic capacity by height for unburned (hatched) and burned (stippled) canopies. Note the rapid decline in capacity with height and the steeper gradient of photosynthetic capacity (top : bottom = 3.19) in the taller, more productive unburned sites compared to the unproductive burned sites (1.53). Error bars show 1 SD. Data are from 1989.

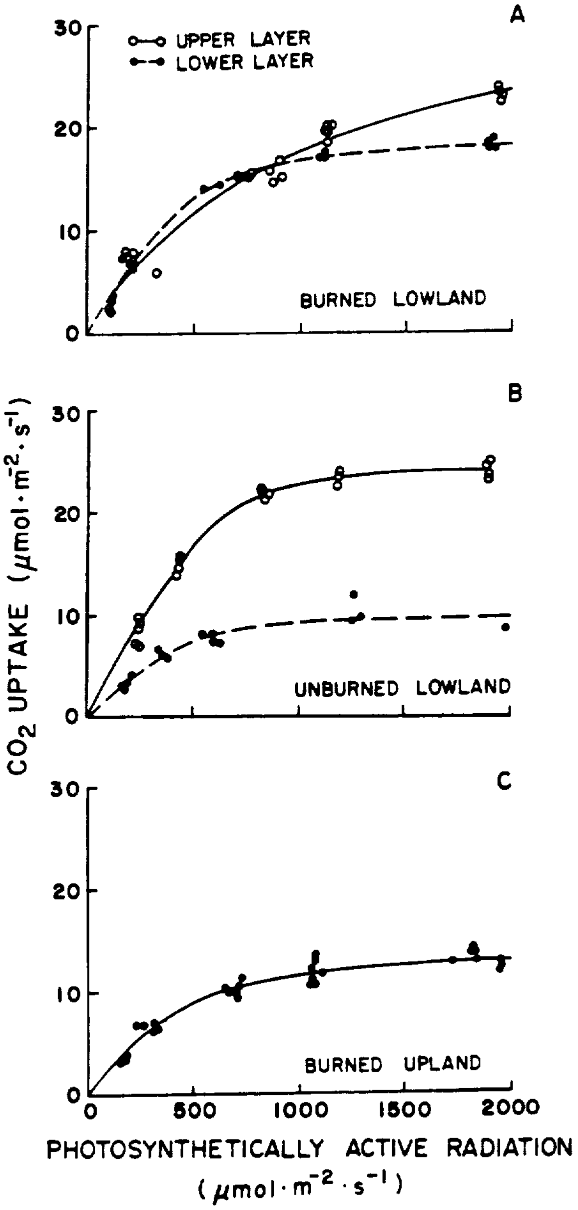


FIG. 10. Photosynthesis vs. PAR by height within the canopy for (A) an annually burned lowland site, (B) an unburned lowland site, and (C) an unproductive burned upland site. In (C), the canopy was sampled as one layer. Data are from 1989.

photosynthetic N gradient index, calculated by first subtracting the inactive N, would be ([12 − 5]/[7.5 − 5]) or 2.8. This ratio is close to the measured ratio of photosynthetic capacities in a productive site (3.2; Fig. 9). This suggests that additional sampling by height for biochemical N fractions would be useful in understanding allocation responses to light extinction within canopies.

The interactions of limiting factors along resource gradients may result in variations in N use efficiency (Hirose and Werger 1987*b*, Seemann et al. 1987, Evans 1989). Nitrogen use efficiency (NUE) is defined as carbon fixed per unit N utilized and can be estimated as the reciprocal of whole plant [N] in herbaceous plants. The aboveground contribution to NUE did not vary within watersheds, since, despite large differences in N allocation by height, whole-canopy [N] did not vary (Table 3). The root contribution to NUE did, however, vary. Our measurements of root [N] in two watersheds (Fig. 5A, B) suggest that whole plant NUE increased in lowland positions due to lower root [N]. The increases in NUE were likely due to reduced water stress, which allowed higher carbon fixation and wider C:N ratios. Higher NUE may also have resulted from the higher [N] in the upper canopy layers of the productive lowland sites, yielding more efficient photosynthesis. While we do not know the mechanism for the large changes in NUE along these toposequences, these differences highlight the significance of plant responses to resource gradients within landscapes (see also Tilman 1985). The effects on root [N] are particularly significant to grasslands since roots influence decomposition and N immobilization and so have feedbacks to ecosystem C and N cycles (Holland and Detling 1990).

Taken together, results reported in this paper demonstrate that the principal factors limiting CO_2 uptake and biomass accumulation varied along resource availability gradients induced by topography and management. Upland sites were almost certainly limited by water or other abiotic stresses (e.g., wind; Knapp 1985). Processes in lowland sites were likely limited by either nitrogen or light. Light limitation was more important in productive unburned sites where considerable PAR is intercepted by dead vegetation.

The effects of climate and climatic perturbations will likely be expressed differently at different sites within the tallgrass landscape as a function of relative resource availability and degree of limitation, as shown by the 1989 production data where low precipitation reversed the relative response of production to burning management. While these results suggest that IPAR may be a useful indicator of canopy photosynthesis and so of ecosystem status, response to climatic perturbation will be modulated by the balance of resource limitation, with different sites responding differentially to changes in light (via cloud cover) and water depending upon interactions between water, N, and other resources. Regional responses must be estimated by integrating over landscape resource gradients using geographic data bases (Burke et al. 1990) or statistical approaches.

Links between resource availability and canopy exchange are required for analysis of atmosphere–ecosystem exchange of energy, water, CO_2, and pollutants (Hicks et al. 1987). Simplifying assumptions relating canopy attributes to proxy or remotely sensed measurements are required for calculation of fluxes from the large areas over which atmosphere–ecosystem interactions occur. Algorithms using intercepted radia-

TABLE 5. Coefficients for photosynthetic light response curves, estimated using a nonrectangular hyperbola. The nonrectangular hyperbola equation has the form: $Ps = (\alpha I + Ps_{max} - \sqrt{(\alpha I + Ps_{max})^2 - 4\,\alpha I Ps_{max}\theta}) \div 2\theta$, where Ps = photosynthetic rate (CO_2 uptake), I = light, α and θ are coefficients describing the curve, and Ps_{max} is the estimated photosynthetic capacity. Sites are as in Fig. 10. Data are from 1989.

Site	Canopy layer	α	Ps_{max}	θ	R^2
Burned lowland	Upper	0.036	34.9	0.000	0.97
Burned lowland	Lower	0.035	19.2	0.843	0.99
Unburned lowland	Upper	0.037	24.7	0.945	0.99
Unburned lowland	Lower	0.020	10.1	0.882	0.90
Burned upland	Single	0.027	14.0	0.707	0.95

tion or satellite correlates (Choudhury 1987, Fung et al. 1987) to compute canopy resistance need to incorporate information on multiple limiting factors (Chapin et al. 1987) to simulate the response of perturbed systems. Principles from evolutionary and physiological studies may provide a basis for the development of these algorithms.

ACKNOWLEDGMENTS

We thank Judith Neubert, Mark Lindquist, Ingrid Burke, Lawrence Duran, Rod Hansen, Mari Nakada, Tracy Benning, Rosemary Ramundo, Jonathan Altenhofen, and John Zachariassen for assistance with field and laboratory work. Piers Sellers, Forrest Hall, Don Strebel, and Ghassem Asrar supported this work through FIFE operations and data systems. Kay McElwain, Dave Jepsen, Linda McFann, and Michele Nelson helped with manuscript preparation. Thanks to the KPRNA for support and hospitality, and to Clenton Owensby for logistical support. The senior author wishes to thank Chris Field and Hal Mooney for many helpful discussions. This research was jointly supported by NSF (BSR 8406628), the Konza Prairie LTER (NSF BSR 8514327), and NASA (NAG 5910) and by a National Research Council Resident Associateship at NASA/Ames Research Center to D. S. Schimel.

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Agriculture, Ecosystems and Environment, 34 (1991) 495–505
Elsevier Science Publishers B.V., Amsterdam

Remote sensing measurements of production processes in grazinglands: the need for new methodologies

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(Accepted for publication 5 July 1990)

ABSTRACT

Dyer, M.I., Turner, C.L. and Seastedt, T.R., 1991. Remote sensing measurements of production processes in grazinglands: the need for new methodologies. *Agric. Ecosystems Environ.*, 34: 495–505.

Remote sensing of grazinglands to obtain estimates of productivity relies entirely upon absorption and reflectance properties of the vegetation and its background to provide accurate qualitative and quantitative values. Interpretations of these signals are highly dependent on vegetation responses to perturbations, such as grazing or alterations in nutrient cycles. If remote sensing models of grassland growth ignore feedbacks derived from grazing animals, or only negative feedbacks are assumed, there is a high likelihood of errors developing during model validation. We review fundamental assumptions made when using remote sensing data from grazing systems and give examples of the problems involved.

INTRODUCTION

Grazinglands are among the most prominent biogeographic regions, with ~25% of the earth's land surface covered by grasslands, savannas and shrub steppes (Laurenroth, 1979). Historically, with perhaps the exception of some forested systems, grazinglands have been the most important single terrestrial ecosystem for human welfare and economics. Thus it is vital that they be managed for long-term optimum returns. However, because of their extent and diversity, it is impossible to monitor them adequately without special tools. Remote sensing provides this potential, but its inherent limitations must be well understood to ensure its full deployment.

Because of easy access and exploitation, a large variety of human societies and cultures have developed in grazinglands throughout the world. In many instances they have been utilized on sustainable bases (Coughenour et al., 1984), but in many regions they are overutilized and are being degraded. Grassland areas of North America must be included in this heavy exploitation category because of economic pressures and land use policies that promote heavy stocking rates on private and public lands.

Grazingland degradation is episodic, often punctuated with short intervals of stress interspersed with relatively long periods of stability. Heavy stocking of grazing animals or outbreaks of pest insects predispose the land surface to major changes in plant species composition, nutrient mineralization, and wind and water erosion, all of which contribute further to the episodic stresses, which vary widely over time and space. The changes themselves derive from climatic factors governing regional and local weather patterns. Additionally, interactions between vertebrate and invertebrate grazers come into play. A large variety of insect species above ground and a combination of macro- and microarthropods and nematodes below ground compete for common resources. This picture is complicated by attempts to control grazingland insects. Control is directed at both long-term eradication of incipient populations and those that erupt periodically into large migrating populations. Perhaps the most prominent control programs are directed at orthopterans in North America and Africa, although other groups, such as lepidopteran larvae and a large variety of below-ground macroarthropods, are also targeted.

Both vertebrate and invertebrate grazers affect grassland species in a like manner. A continuum of plant responses is known for many grasses and recently reports of similar responses for forbs have been published (Paige and Whitham, 1987; Maschinski and Whitham, 1989). This spectrum of responses has been designated the Herbivore Optimization Curve (HOC), a hypothesis introduced by McNaughton (1979) and expanded by Hilbert et al. (1981), Dyer et al. (1982, 1986) and Edelstein-Keshet (1986).

The HOC hypothesis is simple in form. Both empirical and theoretical work show that plant productivity is a function of grazing intensity. Indeed, through positive and negative feedback mechanisms, grazers may account for a major proportion (30–70%) of the variability in plant production within a growing season, making them potentially the single most important factor in ecosystem regulation. In many instances (but not all) as grazers first start to feed, individual plant production processes increase above those in uneaten plants. This increase soon peaks (usually at levels where between 5 and 20% of the plant's tissue is removed; rarely is this herbivory threshold any greater, although McNaughton (1979, 1985) and Williamson et al. (1989) showed much higher levels), after which production falls off rapidly and becomes negative. Thus, the overall response is biphasic, i.e. there is first an increase in productivity followed by a decrease, all as a function of grazing intensity. This plant response may be echoed throughout the community or by various ecosystem components, causing many processes that are linked to basic plant production events to exhibit the same biphasic curve form.

REMOTE SENSING IN GRAZINGLANDS

Both fine- and coarse-grained remote sensing techniques have been utilized to monitor and study grazinglands. Studies using fine-grained techniques focus on local processes (e.g. Curran and Williamson, 1987) through the use of sensors providing spatial resolution of a few meters. Studies using coarse-grained techniques focus on large areas, such as continents or entire biomes, using satellite-based sensors with a spatial resolution of kilometers, such as reported by Tucker et al. (1985).

Perhaps the most intensive single study to collect remote sensing data has been FIFE (First ISLSCP (International Satellite Land Surface Climatology Programme) Field Experiment). This NASA-sponsored study was conducted on the tallgrass prairie of Konza Prairie Research Natural Area (KPRNA) and the surrounding Flint Hills near Manhattan, Kansas, during the years 1987–1989 (Sellers et al., 1989). Many biophysical processes were measured remotely by instruments on the ground and aboard helicopters, fixed-winged aircraft and several satellites. FIFE was designed to monitor conditions over the growing season in what were assumed to be homogeneous locations within a 15×15-km area. The main study did not include a within-growing season experimental plan, although information was collected from burned, unburned, ungrazed and grazed sites that vary annually (Sellers et al., 1989).

One of the ultimate goals of FIFE is to develop the means of obtaining estimates of fluxes of radiation, water vapor, sensible heat and momentum across the plant–atmosphere interface at appropriate temporal and spatial scales for general circulation models (GCMs) that require this data (Sellers, 1989). One such model, the Simple Biosphere Model (SiB; Sellers, 1985, 1987) is a two-stream model (Fig. 1) that describes fundamental energy exchanges within the plant canopy and whose ecosystem interactions are based on an approach reported by Dickinson (1983). In this model, radiation absorption, biophysical control of evapotranspiration, momentum transfer, soil water availability and soil insolation characteristics are computed and combined to give estimates of instantaneous rates of energy flux and status of biotic components of the ecosystem.

The mathematical relationships between the physical components of the model were primarily derived from two transfer pathways (latent and sensible heat fluxes) as exhibited in a plant canopy held in steady state (Fig. 1; Sellers, 1985, 1987). Thus, in principle, by knowing details about incoming and outgoing energy fluxes it is possible to describe in detail plant growth and development. In the model, as in real plant canopies, rates of photosynthesis and leaf water potentials are the most important variables. Variations in these are basic for inferring energy transfers between components within the canopy, the soil and the immediate atmosphere.

In practice, it is relatively simple and straightforward to obtain extremely

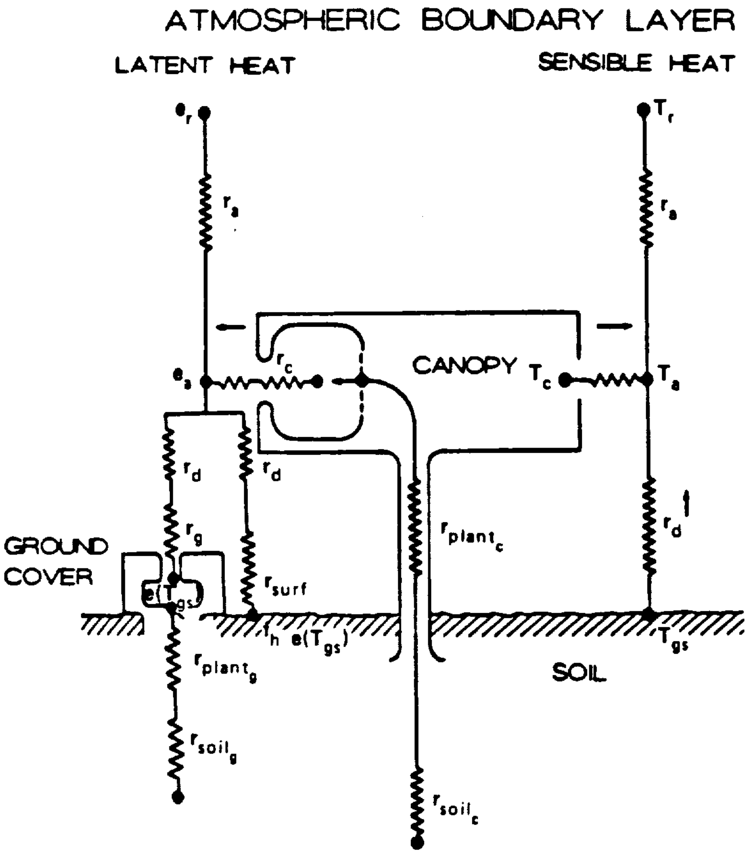

Fig. 1. Simple Biosphere Model (SiB) (Sellers, 1985, 1987) showing major pathways of energy exchange within the soil, canopy and immediate atmosphere, the boundary layer (=atmospheric boundary layer or ABL). On the left side of the model, representation latent heat pathways are shown; on the right side, sensible heat pathways. All incoming radiation is measured by a variety of sensors to provide a total energy perspective. The latent heat and sensible heat levels then integrate a variety of autotrophic and heterotrophic processes from which overall ecosystem function is derived. (See Sellers (1985, 1987) for descriptions of symbol variables shown in the figure.)

accurate measurements of incoming radiation, but much more difficult to measure radiative and momentum transfers across the atmospheric boundary layer. To date, validation of the SiB model has been attempted only in steady-state or unstressed plant communities, although FIFE addressed a spectrum of water fluxes, ranging from those in nearly full field capacity to conditions in total vegetation "dry down", during four 10–20-day sampling periods ((1) May–June, (2) June–July, (3) mid-August and (4) early October) conducted throughout the 1987 growing season. In 1989, there was only one 20-day sampling period (July–August).

Within the FIFE study design, experiments were conducted to investigate the effects of grazing, simulated grazing (mowing) and fertilization throughout the growing season (Turner et al., 1988, 1989; Dyer et al., 1991; Turner, 1991). These studies were designed to determine how grazing and fertilization modify grassland productivity and, more importantly, how effective remote sensing data, principally the Normalized Difference Vegetation Index (NDVI), is in tracing growing season dynamics in grazingland ecosystems (Turner et al., 1988, 1989; Dyer et al., 1991; Turner, 1990). A summary of some of these findings is presented here and interpreted in terms of how effective remote sensing approaches are in following grazingland ecosystem dynamics.

GRAZING DYNAMICS AND REMOTE SENSING: THE BASIC PROBLEM

Absorption of incoming radiative energy is dependent on a variety of physical and biological factors. The quantity and quality of the plant canopy are of primary importance in determining the absorption of photosynthetically active radiation (PAR, 0.4–0.72 μm wavelengths) as well as near-infrared (nir) and infrared (ir) wavelengths. A large variety of sensors has been constructed to provide estimates of this energy absorption by providing measures of the reflected energy in specific spectral bands. For the Multispectral Scanner (MSS) aboard Landsat, the spectral bands are visible (0.5–0.6 and 0.6–0.7 μm) and near infrared (0.7–0.8 and 0.8–1.1 μm). For Landsat's Thematic Mapper (TM), the spectral bands are visible (0.45–0.52, 0.52–0.60 and 0.63–0.69 μm), near infrared (0.76–0.9 and 1.15–1.30 μm), middle infrared (1.55–1.75 and 2.08–2.35 μm) and thermal infrared (10.4–12.5 μm).

Measures of reflectance in individual spectral bands are routinely combined into indexes based on wavelength-specific reflectance characteristics of vegetation. When these indexes are calibrated against types and/or amounts of plant canopy, they become powerful tools for interpreting remotely sensed data. The most useful of these remote sensing indexes have been the NDVI (a combination of ir$-$red/ir$+$red (Tucker et al., 1980)) and a variety of greenness indices (Crist and Kauth, 1986). (For additional details and a more complete description on "Remote Sensing Basics" and "Reflectance Indices", see Wessman, 1991).

As sensors on high-altitude platforms pass overhead, or as an investigator uses a ground-level instrument, a record of reflectances of the earth's surface is obtained which in reality is an instantaneous "snapshot" of any given scene. No new information may be derived until the sensor is in a comparable position at some later time. In vegetated areas, this is a crucial point. The difference in information content between the two sampling periods is often used to infer some vector of biotic or ecosystem response, e.g. growth or senescence in the plant canopy. If between the two measurement intervals there are landscape patches (either fine or coarse grained) that have been grazed by herbivores, and other patches nearby that have been left ungrazed, what is seen in the remote sensing image? During peak activity of the growing season ungrazed areas may show changes in reflectance indicative of increased biomass, while at the same time nearby grazed areas will show changed reflectance signatures from their earlier state(s) that contrast significantly with signals in ungrazed areas. Through correlation techniques it can be deduced that standing crop levels are much higher in ungrazed areas when compared to grazed areas. This then often leads to the conclusion that ungrazed areas are more productive. However, as we have seen from the earlier discussion about the HOC hypothesis, because of the biphasic response potential this conclusion may be completely wrong!

Affirmation of this hypothesis is provided by Dyer et al. (1991) for both mid- and end-of-growing-season sampling periods (Fig. 2). In a controlled experiment using frequent mowing to simulate grazing in a uniform stand of *Bromus inermis* at KPRNA, they obtained evidence of standing crop depletion (a decrease >60%) over the growing season. However, plots mowed heavily to simulate local grazing practices produced up to 44% more than ungrazed controls. Obviously, for this to happen concomitant increases in photosynthesis and growth and development processes had to have occurred. No direct measures of these are available, but other data support this conten-

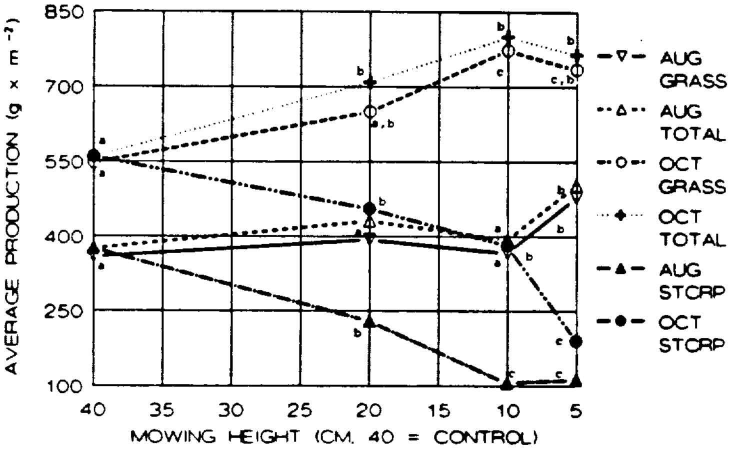

Fig. 2. Results for grass and total biomass obtained from simulated grazing experiments conducted in *B. inermis* plots, Konza Prairie Research Natural Area (KPRNA), Kansas, August and October 1987. For each sampling period, the standing crop was reduced significantly (~60%) by mowing treatments designed to simulate grazing pressure in the tallgrass prairie (40-c=control), 20-, 10- and 5-cm heights), but total productivity (obtained from total offtake during seven treatment dates) showed significant increases (~44%). Means with the same letters are not significantly different, Duncan's multiple range test ($P=0.05$). STCRP=standing crop values for August and October.

tion. Nitrogen uptake was increased dramatically in mowed plots, consistent with the increased plant growth and development hypothesis. Analysis of covariance, with plant biomass and production to date as the covariates (Dyer et al., 1991), showed that total grass productivity was independent of either component. Thus, the conclusion follows that the metabolic state of plants in the treated plots developed as a function of the treatment, which in turn induced unknown internal physiological processes prompting the increases in growth and development.

The most interesting question now is how remote sensing techniques may describe these events. Because only standing crop reflectance values are apparent to the sensors, it is not possible to obtain direct measurements of changes in production rates via the standard visible or non-thermal infrared bands, except by integrating the signals between two successive sampling periods. Thus, it is apparent that unless there are special adjustments made for NDVI or greenness indexes, many grazingland state variables will contain an inherently high error component. Data for two sampling dates (August and October 1987) from the Dyer et al. (1991) study that show effects of mowing and fertilizer application support this viewpoint (Fig. 3).

NDVI values did not show consistent trends within treatment types (grazing and fertilization) or throughout the growing season. Therefore, based on our current knowledge, it appears necessary to develop some degree of calibration for each specific study area. The amount of information required for the calibration process will depend on the complexity of the landscape, what

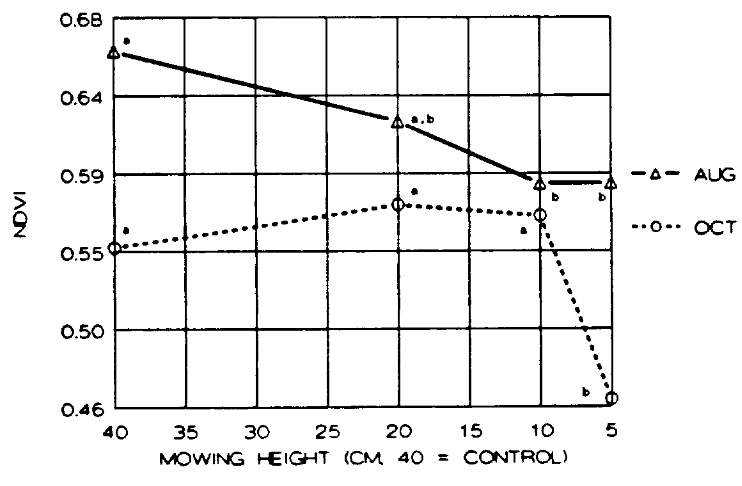

Fig. 3. NDVI from *B. inermis* plots at two sampling dates, KPRNA, plotted against vegetation heights derived from treatments designed to simulate grazing treatments in the tallgrass prairie. NDVI ratios differ significantly between the two sampling periods (August = mid growing season; October = end of growing season) and within plots. Means with the same letters are not significantly different, Duncan's multiple range test ($P=0.05$).

basic data are available from the local area and the degree to which the NDVI model is to be extrapolated.

The main problem encountered with remote sensing studies of grazinglands and the use of NDVI is ensuring that qualitative and quantitative factors associated with canopy reduction, and a concomitant increase in soil exposure, are accounted for as the growing season progresses. Data from the KPRNA site studied by Dyer et al. (1991) are shown in Fig. 4. For calibration purposes, we have chosen to express the independent axis as NDVI. Here we see three regressions covering all mowing treatments: (1) control plots; (2) fertilized plots; (3) the two combined. The best fit regression for the two treatments is a quadratic, however the curve forms are different. The curve for fertilized data is concave; for control plots the curve is convex. The combined curve, which would represent a mixture of fertilized and unfertilized areas in the tallgrass prairie, is a power function (Fig. 4). In the combined curve, variance is moderately high ($R^2=0.621$), reflecting the combination of all treatments. This high variance is a realistic expression because landscapes do not contain homogeneous nutrient patches. Therefore, it is apparent that we must develop an approach to assemble the experience necessary to minimize variance and to reduce as much as possible complex and costly calibration routines.

Detailed information on plant reflectance is required. Even though a great deal of work has been carried out on this subject in FIFE as well as elsewhere, no studies have been designed to understand how grazing affects individual

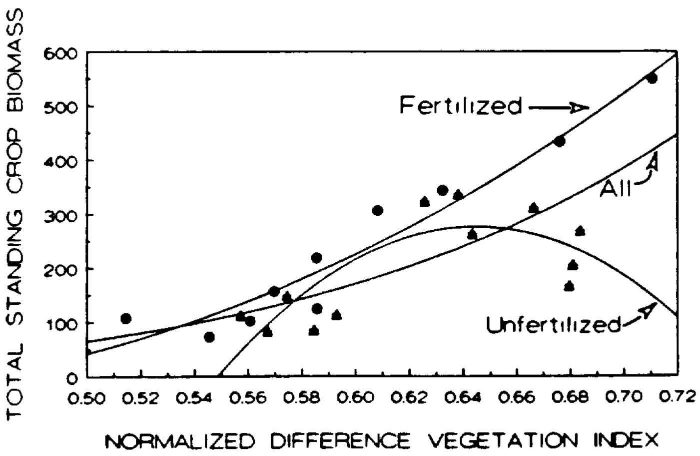

Fig. 4. Scatter diagram of total standing crop from *B. inermis* treatment plots, KPRNA, August 1987, plotted against NDVI. Three regressions are presented giving the best fit for (A) fertilized plots (closed circles, $Y=826.8-4399.4\ X+5662.9\ X^2$, $R^2=0.934$), (B) unfertilized plots (=controls) (closed triangles, $Y=38\,427.1\ X-29\,787.9\ X^2-12\,116.3$, $R^2=0.801$) and (C) all plots ($Y=2502.7\ X^{5.2526}$, $R^2=0.621$).

plant reflective properties. Further, no studies have been conducted to correlate the new physiological state of grazed plants that are contained within the HOC hypothesis with a dynamic picture of changes in reflectance properties.

Lastly, a better model coupling the changing reflectance properties of vegetation and those of the underlying soil must be developed. As grazing alters the plant canopy density and perhaps internal reflectance properties in unknown ways, the substrate, which consists of surface litter and mineral soil, becomes variously exposed. Heute (1988) has called attention to the need for a soil transformation technique (Soil-Adjusted Vegetation Index=SAVI), but has not regarded the inherent biphasic nature underlying the overall problem for grazinglands, even though his correction includes varying canopy biomass densities. Not only will a large variety of soil properties be needed, but these must be coupled with properties in the canopy that are induced by grazing.

Even after all these criteria are satisfactorily explained, it will be necessary to address another problem, perhaps more daunting than those discussed above. Variables measured for the SiB model in microsite conditions must be coupled with those in the HOC model and extrapolated to larger components in the landscape. This step is crucial, for without it, it will not be possible to obtain information on momentum transfers through the plant canopy to the boundary layer. This will be particularly important for gaseous exchanges. With current approaches, which do not account for the HOC model, or for either short- or long-term lag effects in transformations of stored energy components, such transfers can only be measured with a high degree of uncertainty on both fine- and coarse-grained ecological scales. Thus, grazers (types and densities), canopy responses, reflectance properties of plants, and the physical parameters of perturbed canopies and the underlying substrate must all be combined in a new model to attain acceptable measures of grazingland dynamics.

This series of highly detailed studies will have direct implications for understanding crucial interactions among plants and heterotrophs for studies on "Global Change and Terrestrial Ecosystems", one of the principal core projects being planned by the International Geosphere–Biosphere Programme (IGBP) (1988).

The total effects of grazing, or defoliation, are less known for other ecosystems, but it is highly likely that similar conditions exist for forests and agricultural lands. In these ecosystems, a large variety of herbivorous and sucking insects perform basically the same role in herbaceous removal that large ungulates perform in grasslands; the only difference is the visibility of the two groups of heterotrophs.

SUMMARY

A large amount of within-growing season productivity in grazinglands may be governed by grazers, which can be explained by the HOC hypothesis.

Standing crops of grassland vegetation are reduced by grazing, but total production may either increase or decrease, depending on grazing intensity. Because remote sensing approaches obtain a series of "snapshots" of the earth's surface, they can only measure the decrease in standing crop, thus missing the main dynamics within the ecosystem. The error margins, which for some processes may be as much as 100%, are further increased by the role of nutrients and their variability in grazingland ecosystems.

Remote sensing models have been constructed around unperturbed ecosystem dynamics. Because of the biphasic ecosystem responses induced by grazers, there must be approaches developed to account for these impacts, which affect both biomass and gaseous exchanges, otherwise variability in measures of total system function will remain unacceptably high. Such conditions associated with insect defoliation probably exist in other ecosystems, such as forests and agriculture, but their exact nature is much less known.

ACKNOWLEDGMENTS

This paper has focused on research work conducted at Konza Prairie Research Natural Area, Kansas, a preserve of the Nature Conservancy. It was supported in part by NASA Grant NAG 5-897 and NSF Long-term Ecological Research Grant BSR-8514327 to Kansas State University, and NSF Grant BSR-8904632 to M.I. Dyer.

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APPENDIX I

Ecological Applications, 1(4), 1991, pp. 443–452

MOWING AND FERTILIZATION EFFECTS ON PRODUCTIVITY AND SPECTRAL REFLECTANCE IN *BROMUS INERMIS* PLOTS[1]

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Abstract. Experiments were conducted to examine the potential role of grazing on ecosystem-level parameters as part of the NASA-sponsored First ISLSCP (International Satellite Land Surface Climatology Programme) Field Experiment (FIFE) conducted at Konza Prairie Research Natural Area in 1987. Here we report results of one experiment conducted in a field consisting primarily of *Bromus inermis*, a cool season C_3 grass. The experiment involved four simulated grazing components (unmowed control, 20-, 10-, and 5-cm mowing heights) and fertilization (untreated control and ammonium nitrate application). The plots were mowed to ground level and raked in April, following which they were mowed seven times during the growing season from May to October. Biomass production, N production, and spectral reflectance data were collected with a hand-held radiometer throughout the growing season, with standing crop estimates taken at two periods (7 August [day 219] and 27 October [day 300]) to correlate with the remote sensing information base.

Standing crop values of mowed plots were as much as 67–70% lower than controls, but they produced significantly larger amounts of both biomass and total N. Maximum season-long production values in the mowed plots were ≈43% above controls, with major differences developing as a result of fertilization. Fertilized plots produced 67% more foliage than unfertilized plots. Our data show over-compensatory growth as a result of the simulated grazing treatments.

Indexes (NDVI [normalized difference vegetation index] and greenness) derived from the reflectance data were poorly correlated with biomass. The correlation of NDVI with N content of the canopy foliage was somewhat stronger, particularly if stratified by mowing class. NDVI was a better predictor of vegetation status than the greenness indexes, but in plots simulating heavily grazed areas where leafy vegetation was sparse and soil became more visible from above the canopy its utility decreased significantly.

Key words: Bromus inermis; *multispectral scanner (MSS); NDVI and greenness indexes; N fertilization; remote sensing; simulated grazing stresses.*

INTRODUCTION

Grazing ungulates influence many patterns and processes in grassland ecosystems (Dyer et al. 1982, McNaughton 1985). Depending upon the physiographic province, the herbivore community, and intensity and timing of grazing pressure, a large variety of grassland systems develop as direct and indirect responses of nutrient relocation (Woodmansee 1978) and alternative management practices (Parton and Risser 1979, Risser et al. 1981).

The overall impact of removal of plant tissue from the community has been debated widely (Dyer et al. 1982, 1986, Belsky 1986, 1987, Edelstein-Keshet 1986, McNaughton 1986, Paige and Whitham 1987, Maschinski and Whitham 1989). The basic questions are: (1) how do individual plants of various grassland species respond to being grazed, and (2) how do these individual responses become aggregated to represent productivity of a grassland landscape affected by grazing? These then lead to the question: is there a general response, in which case all plants are affected negatively, or are there intermediate or ultimate states wherein some species may redirect their short- and long-term responses to adjust positively to grazing pressures? Several recent reports (Paige and Whitham 1987, Gold and Caldwell 1989, Maschinski and Whitham 1989, Williamson et al. 1989) suggest a continuum of responses that describe the range of responses predicted by the Herbivore Optimization Curve (HOC) hypothesis (McNaughton 1979*a*, Hilbert et al. 1981). More recently, laboratory investigations on carbon source–sink relationships show that grasses may respond to grazing nearly simultaneously with the grazing event (Dyer et al. 1991). Furthermore, the responses were related to ecotypic development as a function of

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[1] Manuscript received 12 February 1990; revised 4 February 1991; accepted 6 February 1991.

long-term grazing history, suggesting that herbivores may impose differing carbon allocation pressures on grass populations (Dyer et al. 1991).

While many laboratory and small-plot studies report both positive and negative feedbacks following herbivory, the question for events in landscapes is still open. Contrary to conclusions reached by Belsky (1986), there are insufficient data in the range science literature to make an adequate assessment of the overall response of grasslands to grazing. The problem is simply this: (1) reports of grazing effects from managed systems are from heavily stocked pastures dedicated to short-term production (these stocking rates are varied in space and time but almost without exception can be considered heavier than pre-historical levels), and (2) long-term permanent exclosures established to ascertain effects of stocking rates in standard grazing lands practice cannot be used as controls. Ironically, these exclosures no longer represent the system they were established to monitor because of the exclusion of large-animal influences, which is one of the main ecosystem processes responsible for maintenance of grassland ecosystems in steady-state conditions. Conditions for controls must be established using either movable exclosures (McNaughton 1979*a*) and/or the analytical approach of Hilbert et al. (1981).

The only way we know to determine the true impacts of grazing is to establish well-controlled experiments involving grazing and simulated grazing (clipping or mowing), and combine these with methods for extrapolating the information to the landscape. As we indicated above, for grazing studies per se, it is necessary to conduct work with movable exclosures (McNaughton 1979*a*), and for experiments simulating grazing (necessary to control pattern diversity problems) one must examine both intensity and frequently in large, complex, expensive and difficult-to-conduct factorial plot designs (Turner et al., *in press*). Lastly, to extrapolate the information to ecosystem and landscape dimensions, a combinations of process information, simulation models, and remote sensing tools is essential.

McNaughton (1976, 1979*b*), working in the Serengeti Grasslands, was one of the first to apply remote sensing techniques to landscape-level assessment of the influences of grazing. Remote sensing also has been used to examine other coarse-grain features in grasslands, such as surface temperatures in burned and unburned areas (Asrar et al. 1988), or soil moisture variations along randomly located gradients (Schmugge et al. 1987, 1988). The basic research necessary to utilize remote sensing to provide estimates of micro- and mesoscale long-term productivity or the impact of grazing is just now being assembled (Schimel et al. 1991, Seastedt and Briggs, *in press*). Recently Kanemasu et al. (1989) and Goward et al. (*in press*) have demonstrated the utility of estimating not only plant biomass, but also such parameters as absorbed photosynthetically active radiation (PAR) using the Normalized Difference Vegetation Index (NDVI). Most analyses, however, use cumulative NDVI based on a time series of coarse-grained satellite images, vs. a "snapshot" obtained from a single satellite image. As satellites capable of taking relatively fine-grained images, such as SPOT (20-m pixels) or LANDSAT TM (30-m pixels) have either infrequent coverage of an area (and/or are expensive to obtain) the need to evaluate exactly how much information can be extracted from single images is an important, albeit preliminary, step for landscape studies. Therefore, microsite responses to grazing or simulated grazing and the protocol for scaling-up these more detailed data into landscape levels need to be established.

This report explores the effects of mowing and nitrogen amendment on a relatively homogeneous community in the tallgrass prairie, and provides information on spectral reflectance in a field experiment to study constraints on ecosystem responses. The work is part of an array of corollary experiments involved with mowing and large-herbivore grazing in the native tallgrass prairie ecosystem, with additional results reported elsewhere (Turner et al., *in press*).

METHODS AND MATERIALS

This experiment was conducted during the 1987 growing season in a 20-ha field containing a nearly pure stand of *Bromus inermis* ≈2 km east of the headquarters on the Konza Prairie Research Natural Area (KPRNA) near Manhattan, Kansas. The design was a 4 × 2 factorial (classes were mowing height × fertilizer; mowing levels were control [no mowing], 20-, 10-, and 5-cm heights; fertilizer levels were control with no N amendment, and a 10 g/m^2 N amendment [ammonium nitrate pellets]) with three replicates in each block. Each replicate plot was 5 × 5 m. The plots were mowed and ranked in early April (day 100) and mowing treatments were conducted seven times during the growing season (days 131, 149, 176, 194, 231, 254, and 300). Estimates of biomass removed were obtained at each mowing. At two dates (7 August [day 219] and 27 October [day 300]) estimates of standing crop of the vegetation were obtained from each plot. Production to day 219 and day 300 was calculated by summing biomass removed at each mowing with standing crop at the August and October dates.

Plant material was transported to the laboratory and dried to a constant mass, ground to pass through a 425 μm mesh screen and digested using a micro-Kjeldahl procedure. A Technicon Autoanalyzer was used to determine total N.

At six intervals (days 149, 176–177, 194, 217–219, 254, and 300), often just before the plots were mowed, three spectral reflectance measurements were obtained from each plot using a four-channel Exotech 100-A instrument. The instrument was calibrated against laboratory standards by Goddard Space Flight Center (NASA) scientists in conjunction with the FIFE study (First ISLSCP Field Experiment) of the Konza Prairie as part of the ISLSCP (International Satellite Land

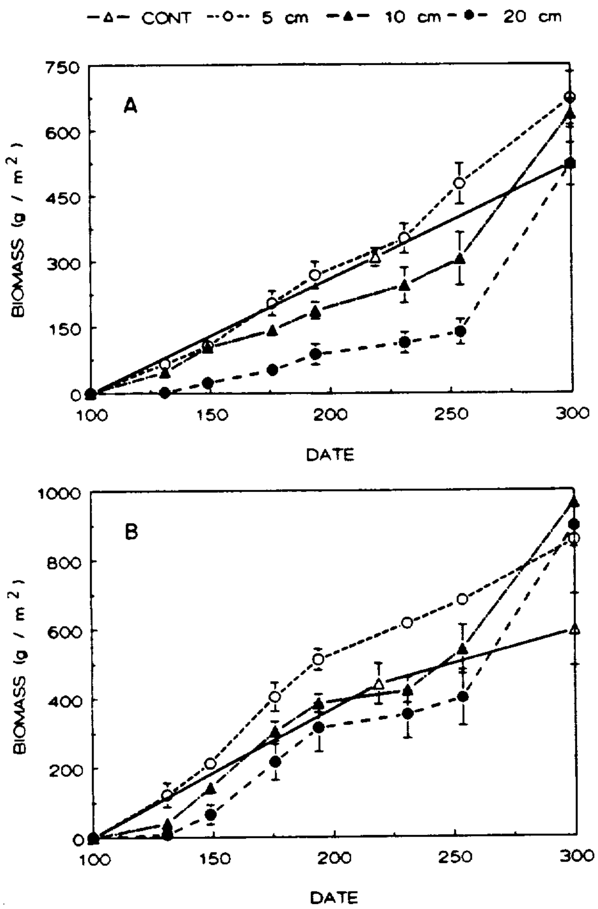

FIG. 1. (A) Cumulative biomass harvest for unfertilized *Bromus inermis* plots on Konza Prairie Research Natural Area (KPRNA) during 1987 NASA-sponsored First ISLSCP Field Experiment (FIFE). (B) Cumulative biomass harvest for fertilized *B. inermis* plots on KPRNA. Means ±1 SE are shown.

Surface Climatology Programme) project (Sellers et al. 1988). All our data were collected between 0900 and 1200 Central Standard Time. Channels used were 1 (0.5–0.6 μm), 2 (0.6–0.7 μm), 3 (0.7–0.8 μm), and 4 (0.8–1.1 μm); the instrument was held in a portable frame 1.5 m above the ground, giving a 15° circular angle of view impinging an $\approx$0.1-m^2 plot.

Linear regressions were used to test influences of physical features in the field on spectral reflectance characteristics. Dependent variables were the computed Normalized Difference Vegetation Index (NDVI $= [ir - r] \div [ir + r]$ or [channel 4 − channel 2] ÷ [channel 4 + channel 2]), and greenness indexes that have their origin in the methods of Kauth and Thomas (1976) and subsequently used widely (Crist and Kauth 1986). One greenness index was taken from Weiser et al. (1986), which has been developed further by Asrar et al. (1986), and the second was derived from a Principal Component Analysis (PCA) of the data collected during this study. The independent variables were total biomass (grams per square metre) and N content of vegetation (percent of total dry biomass). Analysis of covariance, using total biomass as the covariate, was used to examine variation in reflectance within and among the plots; Duncan's multiple range test was used to test differences in class means ($\alpha = .05$).

Analysis of variance, analysis of covariance, and regression tests to determine mean differences in the experimental studies were conducted with SAS packages for microcomputers (SAS 1988) through a license to Kansas State University.

RESULTS

Production dynamics

Biomass production.—The main model of the ANOVA of the season-long, cumulative biomass harvest showed highly significant variation ($F = 34.63$; df = 15, 51, $P < .0001$) with highly significant differences between days ($F = 49.49$; df = 8, 51, $P < .0001$), treatment effects due to mowing ($F = 14.21$; df = 3, 51, $P < .0001$), and fertilization ($F = 43.45$; df = 1, 51, $P < .0001$). Means (± one standard deviation) of the harvest data for unfertilized (controls) and fertilized classes are shown in Fig. 1. In the unfertilized class (Fig. 1A) cumulative biomass for 5-cm (664.4 g/m^2) and 10-cm (629.0 g/m^2) mowing treatments were 22 and 29% greater than the unmowed controls (514.8 g/m^2); the 20-cm treatment showed the same level of productivity as controls ($P = .05$). In the fertilized class (Fig. 1B) cumulative biomass for all mowing treatments (849.2–954.8 g/m^2) was much higher (45–63%) than unmowed controls (585.2 g/m^2). Over the entire growing season the fertilized class produced 67% more than the unfertilized ($P = .05$).

By 7 August the overall mean production level was $\approx$53% of the total production for the growing season, with $\approx$95% of the total biomass being *Bromus inermis*. For both the August and October sampling dates, significant nonlinear relationships developed among treatments ($P < .01$, Fig. 2). The plots mowed to 5 and 10 cm produced more than all others over the entire growing season (the 10-cm plot = 43% > controls, $P < .05$) with the 5-cm mowing class showing the greatest production in August (34% > controls, $P < .05$) (Fig. 2).

As noted above, the application of N caused significant differences (Fig. 3). N-treated plots produced significantly more than control plots ($P < .0001$); at midseason nitrogen-fertilized plot production was 52% greater than controls ($P < .05$), and at the end of the growing season it was 41% greater ($P < .05$). Unmowed, fertilized plots produced 13.7% more than unfertilized controls. Productivity for the 10-cm fertilized plots was 43.7% higher than the 5-cm unfertilized plots, the two representing the highest cumulative production for fertilized and unfertilized treatments, respectively. No mowing height × fertilizer interactions were detected.

Standing crop.—Standing crop for all plots, measured 7 August to provide background information for

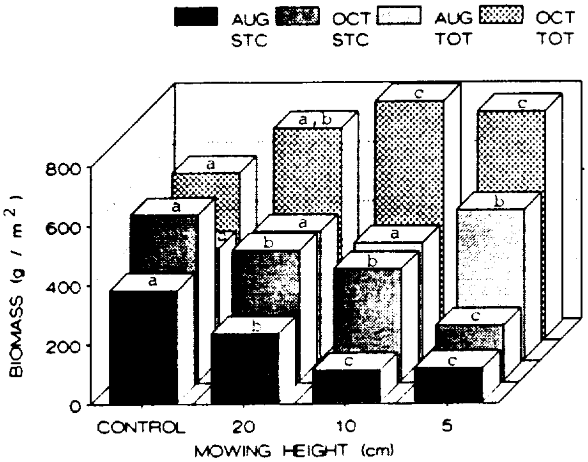

FIG. 2. Standing crop biomass (STC) and biomass produced to date (TOT) on *Bromus inermis* plots on KPRNA at day 219 (7 August 1987) and day 300 (27 October 1987). Within STC or TOT categories for the 2 mo, bars containing the same letters are not significantly different (Duncan's multiple range test, $P = .05$).

the remote sensing work, showed highly significant differences ($P < .0001$), with values nonlinearly related to mowing height treatment (Fig. 2). Total standing crops were reduced significantly by the mowing treatment (5-cm height was reduced 70% compared to controls, $P < .05$, Duncan's multiple range test, Fig. 2). No fertilizer effect was observed ($P = .774$). The overall picture for October was much the same (Fig. 2). Mowing effects showed a significant decrease ($P < .0001$), with the 5-cm height reduced 67% compared to controls ($P < .05$) (Fig. 2). No fertilizer effect was observed ($P = .07$).

Nitrogen production.—Nitrogen content (as percentage of leaf dry biomass) showed significant nonlinear variation throughout the growing season ($F = 42.59$; df = 7, 149, $P < .0001$) and was different among unfertilized and fertilized plots ($F = 75.01$; df = 7, 149, $P < .0001$) and mowing treatment ($F = 8.08$; df = 3, 149, $P < .0001$) (Fig. 4A, B). Even though only three sampling dates are available for the unmowed treatment class, % N was significantly lower than any of the mowed classes ($P < .05$). The 20-cm mowing class was significantly lower than the 5- and 10-cm classes ($P < .05$), which did not differ in their responses (Fig. 4A, B).

Cumulative N production, derived from the season-long harvest data, showed highly significant variation in an ANCOVA using total biomass at each sampling period as the covariate. Total production varied significantly by date ($F = 4.38$; df = 7, 51, $P = .001$) (means by date: day 300 = 17.54 g/m^2; 254 = 15.02; 231 = 3.68; 219 = 12.06; 194 = 11.92; 176 = 8.93; 149 = 5.1; and day 131 = 2.02 g/m^2); by fertilizer treatment ($F = 11.55$; df = 1, 51, $P = .002$) (fertilized class = 16.36 g/m^2; unfertilized class = 5.83 g/m^2); and by mowing treatment ($F = 7.53$; df = 3, 51, $P = .0005$) (5-cm mowing height = 15.87 g/m^2; 10 cm = 11.64; 20 cm = 6.86, and controls = 6.74). (The 5- and 10-cm classes were significantly different from each other and from the other two classes [$P < .05$]; the 20-cm and control classes were not significantly different [$P > .05$].) Maximum N production over the entire growing season was in the 5-cm, fertilized class (cumulative total N = 35.29 g/m^2), the least was in the unfertilized control class (5.72 g/m^2). There also was a significant interaction between fertilizer and mowing treatments ($F = 7.26$; df = 3, 51, $P = .0006$).

Remote sensing measurements

Normalized difference vegetation index.—NDVI showed significant differences by date throughout the growing season ($F = 37.75$; df = 6, 167, $P < .0001$), fertilization ($F = 57.19$; df = 1, 167, $P < .0001$), and mowing treatment ($F = 39.62$; df = 3, 167, $P < .0001$) (Fig. 5A, B [n.b., to avoid clutter, averages of three replicate plots are shown in the figures; the ANOVA was conducted on all values]). Mean values for control and 20-cm classes were not different ($P > .05$), but means for the 10- and 5-cm treatments were significantly different from one another and from the other two mowing classes (control > 20 cm > 10 cm > 5 cm, $P < .05$). Regressions showed that a parabolic relationship exists for NDVI in unfertilized plots with widely varying goodness of fit (Fig. 5A: r^2 for controls = 0.822; 20 cm = 0.791; 10 cm = 0.195; and 5 cm = 0.781), but decreasing linear relationships converging on conditions at the end of the growing season are apparent for the fertilized plots, with even wider variation in the regression fit (Fig. 5B: r^2 for controls = 0.808; 20 cm = 0.66; 10 cm = 0.282; and 5 cm = 0.132).

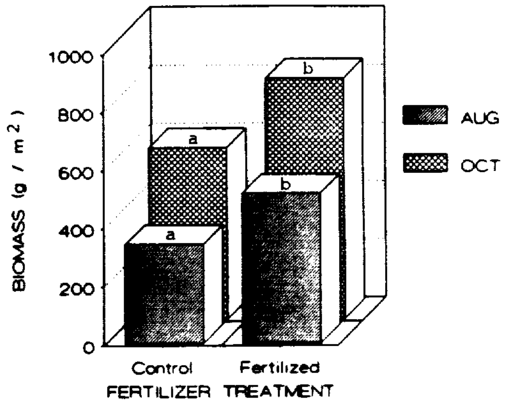

FIG. 3. Production values for total biomass in fertilized and unfertilized (=control) *Bromus inermis* plots on KPRNA, 1987. Data are shown for 7 August and 27 October sampling dates. Bars within August and October data sets are significantly different (Duncan's multiple range test, $P = .05$).

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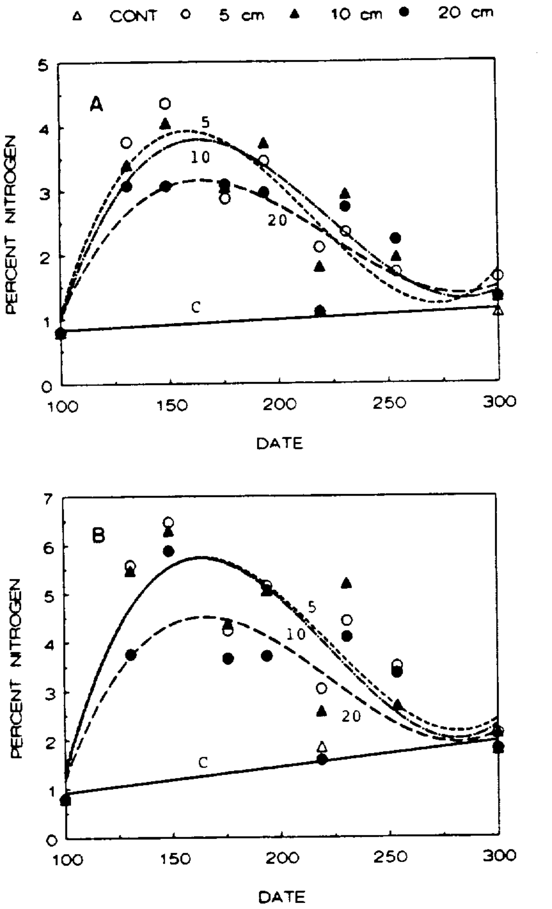

FIG. 4. Changes in nitrogen content of leaves during the growing season in unfertilized (A) and fertilized (B) *Bromus inermis* plots on KPRNA, 1987. Polynomials are best fit curves for each of the mowing classes. Control plots were sampled on two dates only (7 August and 27 October). Initial conditions were assumed to be 0.8% N (T. R. Seastedt, *unpublished data*).

In Fig. 6, NDVI is compared to biomass values collected from all plots on days 219 (7 August) and 300 (26 October). For these data there were significant differences between dates ($F = 23.21$; df = 1, 47, $P < .0001$), no differences for fertilizer treatments ($P > .05$), and significant differences for mowing treatments ($F = 4.91$; df = 3, 47, $P = .005$) (Fig. 6A, B). Fig. 6A also shows that the slope for NDVI plotted against biomass was zero. When differences among dates are examined (cf. regressions for August and October, Fig. 6A) or if mowing treatments alone are examined (Fig. 6B) slightly more predictable relationships emerge. Inspection of the patterns between the various treatments suggests that overall there is a lack of consistent response. The ANOVA showed that responses for the control, 20-cm, and 10-cm treatments were not significantly different ($P > .05$), but that the response for the 5-cm treatment was significantly different from all others ($P < .05$) (Fig. 6B).

A significant relationship developed between NDVI and percent foliar nitrogen over the entire growing season ($F = 35.45$; df = 1, 112; $P < .0001$), but variance was relatively high ($r^2 = 0.252$). Fertilization showed an effect on relationships between the two variables. (For unfertilized plots $F = 3.99$; df = 1, 55, $P = .05$, $r^2 = 0.069$; for fertilized plots $F = 23.78$; df = 1, 56, $P < .0001$ [$r^2 = 0.302$] [Fig. 7A].) In Fig. 7B the effects of mowing treatment are shown. Controls showed no relationships between the two variables ($F = 1.24$; df = 1, 11, $P = .291$, $r^2 = 0.11$), but there were highly significant relationships for the other three classes (20 cm, $F = 24.99$; df = 1, 32, $P < .0001$, $r^2 = 0.446$; 10 cm, $F = 34.06$; df = 1, 31, $P < .0001$, $r^2 = 0.532$; and 5 cm, $F = 20.91$; df = 1, 35, $P < .0001$, $r^2 = 0.381$). The intercept for the controls did not differ from those of all other classes ($P > .05$), but intercepts for each of the other treatment classes were significantly different from one another ($P < .05$) (20 cm > 10 cm > 5 cm, Fig. 7B).

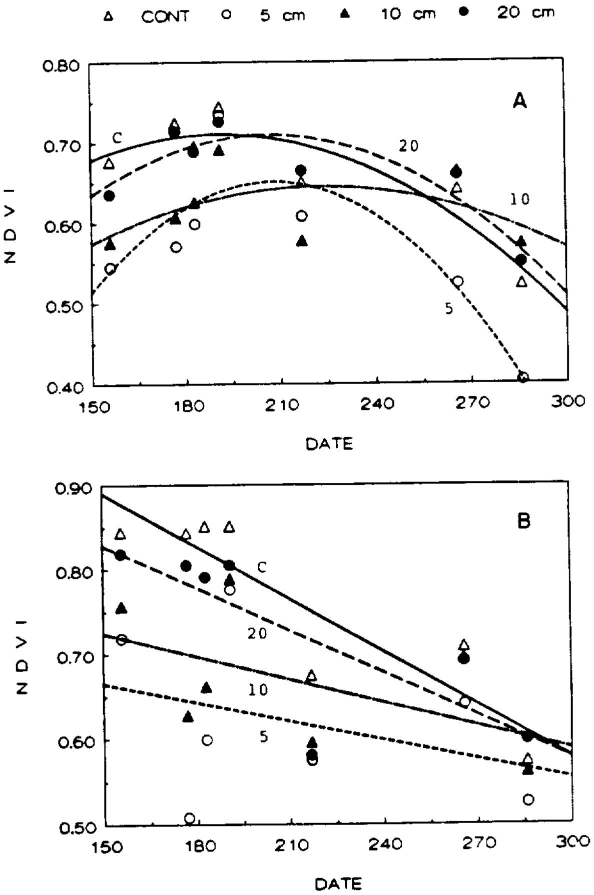

FIG. 5. Normalized difference vegetation index (NDVI) by sampling date in unfertilized (A) and fertilized (B) *Bromus inermis* plots on KPRNA, 1987. Best fit regressions are presented for each of the mowing classes. Unfertilized control plots demonstrated parabolic responses, fertilized plots showed decreasing linear responses converging on a common point at the end of the growing season.

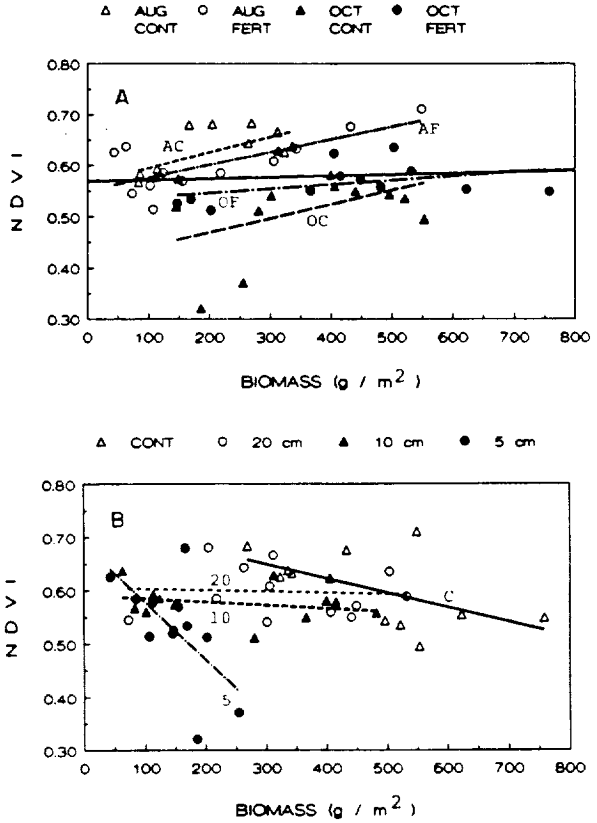

FIG. 6. Normalized difference vegetation index (NDVI) plotted against standing crop biomass levels for the 7 August and 27 October sampling dates. Differences in relationships were apparent between the two months, but not for fertilizer treatment (A). The overall regression slope (solid line) was not significantly different from zero ($P > .05$). NDVI values varied significantly according to mowing class ($P < .05$) (B).

Greenness indexes.—For the August sampling date the principal components equation for the Exotech 100 instrument was (Ch = Channel):

$$GN = 0.5305 \text{ Ch } 1 + 0.4394 \text{ Ch } 2 + 0.5164 \text{ Ch } 3 + 0.5087 \text{ Ch } 4. \quad (1)$$

For October the equation was:

$$GN = 0.5327 \text{ Ch } 1 + 0.4971 \text{ Ch } 2 + 0.5371 \text{ Ch } 3 + 0.4250 \text{ Ch } 4. \quad (2)$$

In August the Weiser et al. (1986) greenness index showed no significant difference due to mowing ($F = 2.50$; df = 3, 23, $P = .099$), but there was a significant difference due to fertilizer treatments ($F = 4.93$; df = 1, 23, $P = .05$). In October the index showed no significant difference for mowing ($F = 2.94$; df = 3, 23, $P = .067$), but there was a significant fertilizer effect ($F = 7.12$; df = 1, 23, $P = .018$). No mowing × fertilization interactions were observed for either sampling date. Despite the statistical association shown for fertilizer treatments, regression analyses showed no significant relationships between the greenness index and either standing crop biomass or fertilizer effect ($P > .05$).

The greenness index described by the principal components analysis conducted for this study showed no significant differences for either date or fertilizer treatment ($P > .05$). Mowing showed a significant difference ($F = 4.03$; df = 3, 47, $P = .013$), with a complex pattern in the response (5 cm > control and 10 cm > 20 cm). No mowing × fertilization interactions were observed, and regression analyses found no significant relationships between this greenness index and standing crop biomass, fertilization, and percent N ($P > .05$).

DISCUSSION

Plot productivity

In conjunction with the FIFE study on the Konza Prairie Research Natural Area (KPRNA) we have used field experiments and remote sensing to analyze grassland ecosystem processes. Because there has been no previous remote sensing work conducted on the impacts of consumers (grazing) on productivity in this tallgrass prairie, we have focused on this approach.

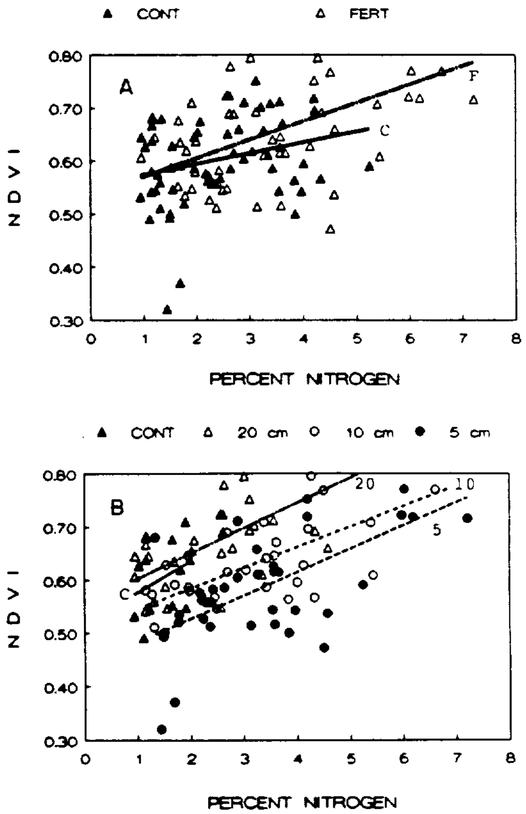

FIG. 7. Normalized difference vegetation index (NDVI) plotted against percent N in the vegetation. Regression slopes varied significantly ($P < .05$) by fertilization treatment (A) and mowing class (B).

Research was designed to ask whether ecosystem-level effects can be detected by utilizing remote sensing approaches, ranging from ground-level to high-altitude imagery, including that from satellites. This work examines the least complex system at Konza Prairie, a relatively homogeneous C_3 *Bromus inermis* community planted in uniform deep bottomland soils. Weather patterns during the 1987 growing season were unusually wet, causing continuous growth of *B. inermis,* which usually senesces during summer dry periods more often encountered on the Konza Prairie. Thus we were able to provide a growth pattern to our field experiments relatively unpunctuated by the effects of a major summer "dry down," which is more often the norm.

Our results show conclusively that *B. inermis,* as is the case with many C_4 and C_3 grasses, responds to repeated grazing (here mowing was used as a surrogate of grazing) by altering productivity when compared to ungrazed controls. The type of change is a function of the degree of removal and has been described empirically and theoretically by several workers in terms of the Herbivore Optimization Curve (HOC) (McNaughton 1979*a,* Hilbert et al. 1981, Dyer et al. 1982, 1986, Williamson et al. 1989, and others), as well as in theoretical models of the dynamics of plant quality in response to herbivory (Edelstein-Keshet 1986). The response is known for many different species in grasslands throughout the world. In many cases processes associated with grazing regulate a large amount of the variance in productivity during any one growing season.

The responses to the experiments we describe here were relatively straightforward. Even though standing crop biomass was highest on unmowed control plots, throughout the growing season mowed plots produced more than controls; at midseason the maximum change was +34% by all 5-cm-high plots mowed five times, and by season end was +27% by all 10-cm-high plots mowed seven times. These responses and their values are biologically significant in several ways. They point to the importance of understanding grassland productivity under grazing stress, but also focus attention on the inherent difficulty of determining grassland function by relying on instantaneous measures of biomass, particularly if taken in ungrazed portions of grazed sites, or in grazed pastures if response to grazing is not accounted for.

In addition to a mowing effect, a pronounced fertilizer effect was observed. While no mowing × fertilizer interaction was observed in the ANOVA, overcompensation by all mowing treatments was observed under fertilized conditions. Only the 5- and 10-cm mowing treatments were more productive than the unmowed plots in the absence of fertilizer. Nitrogen availability therefore does appear to be an important component in the over-compensatory response as predicted by Dyer et al. (1986) and Edelstein-Keshet (1986) in theoretical studies, and observed by Coppock et al. (1983), Detling and Painter (1983), Detling (1987), Holland and Detling (1990), Turner (1990), and Turner et al. (*in press*).

Thus, in view of responses that follow the HOC as a function of the mowing classes, and interaction effects between mowing and fertilization, which fit other reported studies (Detling 1987), we have every reason to believe that our treatments have realistically represented what happens in a natural grassland system.

The covariance analyses for the nitrogen assessments are worth special note. Essentially this technique filters out the effect of biomass or productivity on variation due to treatment or seasonal effects. By using biomass as the covariate we are asking if there is a nitrogen effect independent of biomass changes as a function of mowing or fertilizer class. The mowing treatment shows an effect in midseason, but this disappears by the end of the growing season. We then used cumulative biomass values as the covariate (data not presented), and in doing so posed a more abstract question, because the cumulative biomass parameter is not immediately measurable at any point in time, and, as such, served as a surrogate for altered physiological state. Interestingly, we observed much the same result. There was a pronounced fertilizer treatment effect, and the mowing treatments showed effects at midseason, but not at the end of the growing season.

Since the variance in nitrogen concentrations cannot be attributed solely to differences in foliage biomass, grazing alters plant physiology in ways beyond the simple dilution of nitrogen in enhanced biomass. Nothing about the exact nature of these processes can be derived from this study, but by inference internal plant dynamics involving N, such as chlorophyll content (Ramundo et al. 1989) and carbon allocation were affected by fertilizing or mowing. In turn these resulted in biological interactions in the field controlling production dynamics and remote sensing variables. This sequence of events underscores the importance of knowing the hierarchical components of a major ecological problem before it can be understood adequately.

Remote sensing measures

For the two intensive sampling dates (7 August and 27 October) the Normalized difference vegetation index (NDVI) derived from hand-held radiometer data collected for this study detected mowing treatment differences, but was refractory to fertilizer effects, even though the season-long record showed a pronounced association with N (Fig. 7A). The greenness index reported by Weiser et al. (1986) was unresponsive for the *B. inermis* experiment, and the greenness index we developed specifically for the *B. inermis* plots using principal components analysis was only moderately successful in its application.

An analysis of covariance of individual radiometer band values, with standing crop as the covariate, showed that reflectance from the plant canopy is independent of dry biomass per se. This finding reaffirms older reports that structural components alone are not the main basis for determining the amount of absorption or reflectance, but other properties contained within the plant, mainly water and chlorophyll (Tucker 1979), are the determinants. Thus, if biomass (or its equivalent, leaf area) is not the main source of variation, and since N (the main contributor to chlorophyll development) varies according to mowing treatment, it follows that the main controller of remotely sensed radiation is the internal state of the plant. In our experiments we take this to be both the qualitative and quantitative N status within the plant. This is an important factor in measuring canopies that are influenced by grazing. Total instantaneous biomass is reduced temporarily, but at the same time the plant's metabolic status can be increased significantly, one of the net results being that total N is increased. Therefore, changes in leaf area or total biomass that affect absorption or reflectance as a function of grazing may be offset by concomitant changes due to nitrogen or water status. No studies have been performed to work out this complex equation, but our data suggest that these functions are important.

In remote sensing studies instantaneous snapshots are taken of a landscape. At each time such a snapshot is obtained, standing crop biomass is recorded (Figs. 1 and 2). Dynamic representations (season-long primary productivity, for example) are obtained by integrating between successive measurements. However, because physiological and species-level population responses are nonlinear, this does not give an accurate picture of ecosystem dynamics and overall behavior. Fig. 2 provides an example of the basic phenomena as a result of grazing treatments. Instead of a simple reduction of standing crop biomass distributed uniformly throughout grazed areas, the real situation is a patchy landscape with high and low production areas governed by the recent grazing history. Failure to account for this patchy environment can create errors in estimating other ecosystem parameters, such as energy fixation, respiration, and, especially, evapotranspiration. The errors can be significant, as Fig. 2 shows. While high-altitude remote sensors may document grazing land vegetation, much as we provide for *B. inermis* standing crops (Fig. 2), the standing crop picture is an extremely poor representation of overall function in the grasslands.

What is happening physiologically is indicated by data showing productivity increases above controls. The total amount of tissue produced by mowed (grazed) plants is significantly higher, which means that other parameters involved in growth and respiration are also changed concomitantly. Rates of photosynthesis, transpiration, translocation, and several processes associated with rhizosphere respiration are all increased. Products associated with these processes that are released into the surrounding environment, such as CO_2, H_2O, N_2O, and various organic or inorganic molecules, will be changed as well. In some instances there could be increased uptake, in others increased releases. This switching behavior has important implications for regional-level and global-change studies.

The potential overall impact is large. If we assume responses proportional to biomass production, our experimental measurements suggest that metabolic increases in the field may reach levels 40% over controls (measured for the 10-cm mowing height). At the same time this treatment class showed the lowest standing crop (a decrease to ≈70% of controls). If, as is often done, it is assumed that metabolic activities cited earlier are reduced accordingly, erroneous estimates of ecosystem dynamics amounting to >100% can easily come about. In actuality, this is probably a conservative estimate because the plant growth responses are not linear.

The relationship between NDVI and percent foliar nitrogen for different grassland sites deserves comment. In this study it is apparent that the slopes of the season-long regressions of NDVI plotted against nitrogen are positive (Fig. 7). However, in a mowing height and frequency study without the application of N that was conducted nearby on a native tallgrass prairie community, the slopes ranged from zero to negative (Turner et al., *in press*). Because the site conditions were different and because we did not add fertilizer to the tallgrass prairie community, the levels of N incorporated into vegetation in the mowed classes were much less than in the *B. inermis* study (Turner et al., *in press*). As a result, structural biomass became more important than N content in controlling the overall reflectance response and the NDVI ratios in the tallgrass prairie community in contrast to the results reported here for the *B. inermis* study. Equally important, the level of variability for within-treatment classes was much lower. In this study, as we have pointed out earlier, there was a biological interaction between structural biomass and the increased N content for the mowed and fertilized classes, and this interaction provided a higher degree of variability within and between classes. These differences between the two studies further point out the degree of variation one must expect within a landscape framework.

Of the three indexes used in this study, NDVI seems to be the most robust and preferred. Goodness-of-fit characteristics are not as good overall as those presented in other reports (Tucker et al. 1980, 1985, Goward et al. 1986), but it must be noted that we were examining heterogeneity among plots. The Weiser et al. (1986) greenness indexes did not represent biomass variability among our plots at all. This index is the closest generic greenness index for the Konza Prairie (Asrar et al. 1986, Weiser et al. 1986), but it was developed over different soils for a mix of different species. Nonetheless, the fact that it was developed to represent Konza Prairie conditions and did not is disturbing, for that possibly means a different greenness index must be developed for each and every new case, an impractical solution to developing remote sensing techniques to examine ecosystem form and function. Equally surprising was the finding that the greenness index developed from our data base using a PCA did not represent varying conditions among our plots. Thus, we suggest continued use of the NDVI, but with caution in heavily grazed areas because goodness of fit may be reduced considerably with increased patchiness and within-site variability.

Landscape assessments

NDVI indexes often have been developed from undisturbed canopies in microsite conditions and applied to the larger landscape picture. This approach introduces a major amount of uncertainty. For example, as we present in this paper, in grazed systems there is a within-growing-season reduction in standing crop biomass that alters the amount of PAR being intercepted. With heavy grazing, a common management practice in rangelands, LAI often becomes less than one, which means that increasingly less productive plant tissue with a higher albedo and a greater proportion of ground conditions are exposed to incoming radiation. But at the same time, as we have already pointed out, at the physiological process level increased grazing pressures increase relative growth rates and the level of N in the plant tissue, in turn increasing the NDVI index. Thus, values from these sources become integrated in reflectance measurements, often in unpredictable ways. This differential response model is apparent in our experiment.

Perhaps the main problem lies in the fact that system responses are nonlinear and that there is an inherent scale problem involved in using NDVI. While reflectance indexes for unmowed plots and those mowed to ≈½ of full canopy levels were linearly related, canopies mowed to ¼ and ⅛ of controls became transparent to plant stems and soil conditions, causing a nonlinearity in reflectance values that can be transferred mathematically into the indexes. These latter mowing levels are commonly encountered within and among grazed pastures that constitute a relatively fine-grained pattern within the landscape. Thus, not only is there patchiness in the environment at any given time that a single snapshot encounters, but often there are dramatic changes from t_0 to t_{0+n}, where it has been hoped that remote sensing information could help define progression of seasonal dynamics. Instead, the remote sensing information itself may be as variable as the physical components in the spatial/temporal landscape mosaic, thus leaving us with the problem of analyzing these new uncertainties.

These uncertainties, which involve knowing about changing conditions in the canopy and the soil, coupled with the problem of representing total productivity discussed above, must be solved before it is possible to utilize remote sensing for making accurate measurements of grazing effects in grasslands. Parts of this situation have been discussed by Huete (1988) for a variety of soil effects and for areas of the United States Southwest. His suggested solution is to introduce models, such as SAVI (Soil Adjusted Vegetation Index), to account for combinations of vegetation and soil reflectance properties. While Huete (1988) advocates the use of SAVI under a broad array of conditions, no experience exists with employing this technique in the tallgrass prairie under extreme variations, such as those experienced in this study. More recently Hall et al. (1990) have suggested new methods employing the use of the second derivative of the reflectance vs. narrow wavelength function to help solve the problem of correcting for uncontrolled heterogeneity in landscapes. These two ideas need to be tested thoroughly in grassland communities subjected to a variety of grazing pressures. In the meanwhile, NDVI can be considered a useful index for following relatively fine-grained ecosystem processes and patterns, but its overall use needs to have more careful ecological scrutiny than has been employed heretofore.

ACKNOWLEDGMENTS

Many have helped us in this study. Mary Cunningham Gorman, Brenda Sweat Rongish, Sharla Bradley, Gary Wright, T. Dawn Shapley Jackson, Keith Hayward, Stacy Cloughley, Brian Jones, and Sharon Gurtz helped collect the field data. We thank Ghassem Asrar, Dale Reed, Janet M. Killeen, and E. T. Kanemasu for use of equipment and expert advice. Rosemary A. Ramundo provided the N analyses and laboratory coordination. This research was conducted at Konza Prairie Research Natural Area, a preserve of the Nature Conservancy operated by the Division of Biology, Kansas State University. It was supported in part by NASA Grant NAG 5-897 and NSF Long-term Ecological Research Grant BSR-8514327 to Kansas State University, and NSF Grant BSR-8904632 to M. I. Dyer.

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Seasonal Variation of Heterogeneity in the Tallgrass Prairie: A Quantitative Measure Using Remote Sensing

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ABSTRACT: Remote sensing may be a tool to quantitatively measure the change in heterogeneity that takes place in a landscape over a growing season. Seven different SPOT satellite scenes of the Konza Prairie Research Natural Area were analyzed to assess the potential of using textural algorithms as a quantitative measure of seasonal variation in heterogeneity. Unburned watersheds usually have greater heterogeneity than annually burned watersheds. However, the greatest amount of heterogeneity as measured by textural analysis occurs in those areas with a mixture of forest and upland tallgrass prairie. Results suggest that remote sensing textural algorithms, in combination with normalized vegetation difference indices, can provide insight regarding both temporal changes that occur seasonally and the influences of periodic spring fires and management practices on the tallgrass prairie ecosystem.

INTRODUCTION

FIRE IS CONSIDERED a necessary component for the preservation and maintenance of the North American tallgrass prairie (Hulbert, 1969; Owensby and Smith, 1973; Towne and Owensby, 1984). In the absence of recurrent fire, litter accumulates, plant production declines, plant composition changes, and woody species invade (Abrams *et al.*, 1986; Bragg and Hulbert, 1976; Briggs *et al.*, 1989; Knapp and Seastedt, 1986).

Landscape heterogeneity relative to the frequency of fire within a landscape, however, is an important component of understanding the tallgrass prairie ecosystem. Annual burning of tallgrass prairie reduces the diversity of both vegetation and various grassland birds and mammals (Collins and Gibson, in press; Kaufman *et al.*, in press; Finck and Briggs, unpubl data). Gibson (1988) reported on the fluctuation (i.e., non-directional irregular changes induced through yearly climatic variation), regeneration, (i.e., cyclic succession; recovery from a fire), and landscape heterogeneity of tallgrass prairie burned every four years. He reported that vegetation community patterns were related primarily to original landscape heterogeneity and secondarily to the burning cycle. Furthermore, he found that watersheds remain distinct from each other in spite of the same treatment effect (fire).

Allen and Wyleto (1983) reported that the scale of analysis is critical to what is deemed important in determining community composition within the tallgrass prairie. The ability to detect environmental heterogeneity depends on the scale of measurement (Wiens, 1989). For example, climatic fluctuations and watershed differences would represent large-scale effects, fire frequency within a watershed may represent an intermediate effect, while different soil types within a watershed would represent a small scale effect. All of these factors interact within the context of landscape heterogeneity to maintain the tallgrass prairie. Thus, a quantitative tool to measure and aggregate landscape heterogeneity in the tallgrass prairie over various spatial scales as well as under different management plans is needed.

Recovery from spring burning and seasonal growth patterns of an adjacent annually burned (over a period of 15 years) and long-termed unburned (not burned for 15 years) tallgrass prairie is shown in Figure 1. As illustrated, any measure of heterogeneity in the tallgrass prairie must also include a temporal component in addition to a spatial component. Remote sensing, through its repetitive acquisition of digital image data using various types of electromagnetic energy, may provide such a tool. An investigation is therefore warranted of textural algorithms as applied to remote sensing data in an attempt to quantitatively measure heterogeneity of tallgrass prairie landscapes.

Nellis and Briggs (1987) used band ratioing of digital numbers associated with a Landsat Thematic Mapper scene to discriminate between burned and unburned areas within a tallgrass prairie. However, such direct measures of spectral reflectance do not give a quantitative measure of heterogeneity within a landscape unit. In our earlier paper (Nellis and Briggs, 1989), we used texture analysis as a quantitative tool to measure the effect of spatial scale on various landscapes within the Konza tallgrass prairie of Kansas under various management treatments.

Textural algorithms generate a value that can reflect the amount of heterogeneity within a landscape. Such algorithms generally measure the similarity between a central picture element in a subset of the image matrix and the surrounding picture elements in a moving image window.

Texture can also be described as fine or coarse. As spatial patterns become more definitive in an image and extend over many pixels, a coarse texture results (Haralick *et al.*, 1983).

Measures of interdependence of pixels are commonly made by quantitatively examining the variability of pixels within a specified block of picture elements (Haralick and Shanmugan, 1974; Haralick, 1979; Hsu, 1978; Frank, 1984; Wang and He, 1990). However, there is no widely accepted texture measure appropriate for all landscape monitoring applications. Statistical textural features, though, have been used to measure the similarity or differences between a central picture element in a subset image matrix and the block of surrounding elements (Shih and Schowengerdt, 1983). Nellis and Briggs (1989), for example, have used Landsat Thematic Mapper (TM), Landsat Multispectral Scanner (MSS), and density sliced aerial photography to demonstrate the advantages of textural information in combination with reflectance information for improving image classification and interpretability.

The size of landscape features can also bias the texture measure. Landscape unit size is normally adjusted for by selecting a neighbor dimension appropriate for a particular study area. For example, a 3 by 3 picture element neighbor may be more

PHOTOGRAMMETRIC ENGINEERING & REMOTE SENSING,
Vol. 57, No. 4, April 1991, pp. 407-411.

0099-1112/91/5704-407$03.00/0

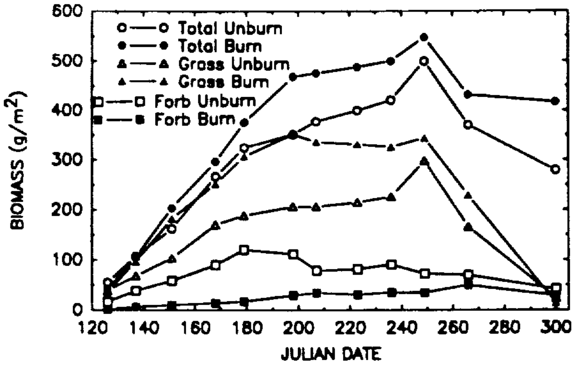

FIG. 1. The seasonal pattern of several components of aboveground biomass on two adjacent ungrazed watersheds on KPRNA--one annually burned and the other a long-term unburned. Solid items = burned site, while clear items = unburned site. Circles = total aboveground biomass; triangles = grass biomass; squares = forbs and woody plant biomass. Total aboveground biomass production includes live grass, forbs, woody plants, and current year's dead biomass.

appropriate in diverse landscapes, and a 10 by 10 window in a homogeneous landscape.

The objective of our study was to use texture analysis as applied to SPOT HRV multispectral data sets throughout a growing season in the tallgrass prairie to monitor the changes in heterogeneity that occur within various landscape units. Texture was determined by measuring the maximum difference between the largest and smallest digital numbers in a landscape unit neighbor (pixel matrix). These values were then used to evaluate the effect on landscape structures associated with various management practices commonly used in the Flint Hills.

STUDY SITE

Konza Prairie Research Natural Area (KPRNA) is a tallgrass prairie located in the Flint Hills region about 10 km south of Manhattan, Kansas (Figure 2). This 3487-ha area is largely native grassland dominated by big bluestem (*Andropogon gerardii*), little bluestem (*A. scoparius*), Indiangrass (*Sorgastrum nutans*), and switchgrass (*Panicum virgatum*). Konza Prairie Research Natural Area is representative of the Flint Hills Upland, a band of rolling hills roughly 70 kilometres wide, extending across Kansas from near the Nebraska-Kansas border south to Oklahoma (Figure 2). The hills were formed by the erosion of the underlying Permian limestone and shale sediments. The hills are characteristically steep-sided with distinctive benches above the limestone members. Soils on slopes and uplands are typically shallow and rocky while larger valleys have deep, permeable soils. Elevation on KPRNA ranges from 320 metres to 444 metres, with most of the land in the range of 366 to 427 metres. Slightly more than six percent of KPRNA is wooded by gallery forest (narrow bands of woody vegetation along the stream channels), dominated by bur oak (*Quercus macrocarpa*), hackberry (*Celtis occidentalis*), and chinquapin oak (*Q. muehlenbergii*).

Under an experimental plan initiated in 1971, different watershed units (catchment basins) were placed under a variety of prescribed burning (mid-April) regimes ranging from annual, 2-, 4-, 10-, and 20-year (long term unburned) intervals (Marzolf, 1988).

MATERIAL AND METHODS

Seven different SPOT HRV satellite scenes (with a 20-meter resolution) of the Konza Prairie Research Natural Area were used to determine the value of textural algorithms for examining seasonal variation in landscape diversity. The HRV SPOT system has three bands of electromagnetic energy sensitivity (channel 1, 0.50 to 0.59 micrometres; channel 2, 0.61 to 0.68 micrometres; channel 3, 0.79 to 0.89 micrometres). Scenes were selected based on cloud cover (less than 5 percent) and zenith view angle (less than 5 degrees). The scenes, collected in 1987 (20 March, 10 April, 01 May, 26 June, 28 July, 13 September, and 30 October), were geometrically co-registered using at least 30 ground points. In addition, to facilitate across-date comparisons, the scenes were radiometrically normalized using pseudoinvariant features and corrected for solar zenith angle after procedures developed by Schott *et al.* (1988) with modifications for use with the HRV SPOT system. These modifications simply involved matching the appropriate SPOT HRV channels with the one suggested by Schott *et al.* (1988) for their work using Landsat Thematic Mapper (TM) data sets. This approach corrected for changes in atmospheric propagation, illumination effects, and sensor response differences in the multitemporal HRV SPOT data. Other factors are more difficult to correct (i.e., shadowing from vegetation), and may have some impact on the resulting digital values used in this analysis.

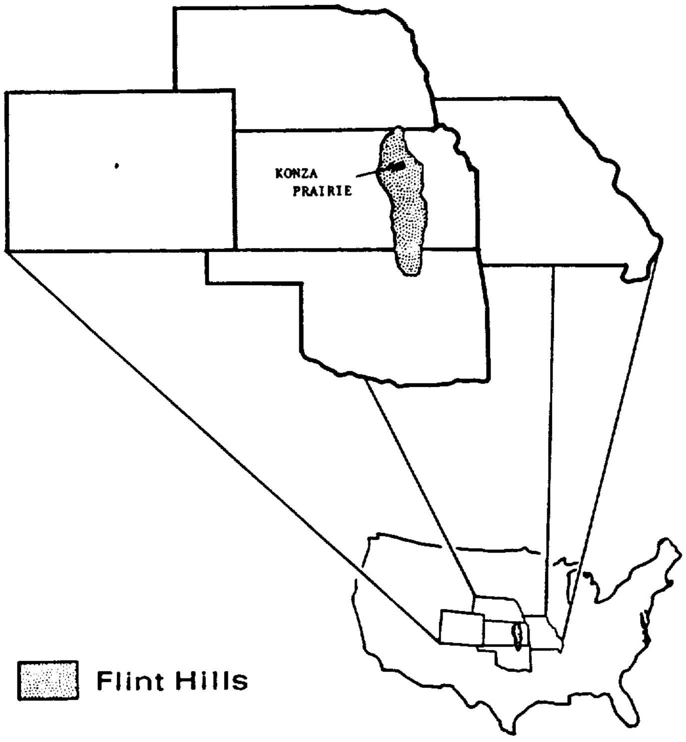

FIG. 2. The Kansas Flint Hills.

Normalized difference vegetation indices (NDVI) of each scene were calculated using the equation

$$(\text{channel } 3 - \text{channel } 2)/(\text{channel } 3 + \text{channel } 2),$$

as NDVI has been successfully used in the Flint Hills for biomass comparisons between burned, unburned, grazed, and ungrazed areas (C. L. Turner, unpubl. data) (Figure 3). A textural contrast algorithm was then applied to each NDVI generated scene. For comparative purposes, the textural algorithm was also applied to each individual channel. The textural algorithm (after Jensen, 1986) involved passing a 3 by 3 window min-max texture operator through each image. The higher the resulting textural number (approaching 256), the greater the degree of contrast or heterogeneity. Textural contrast values were then compared to KPRNA watershed burning treatments and resulting landscape composition.

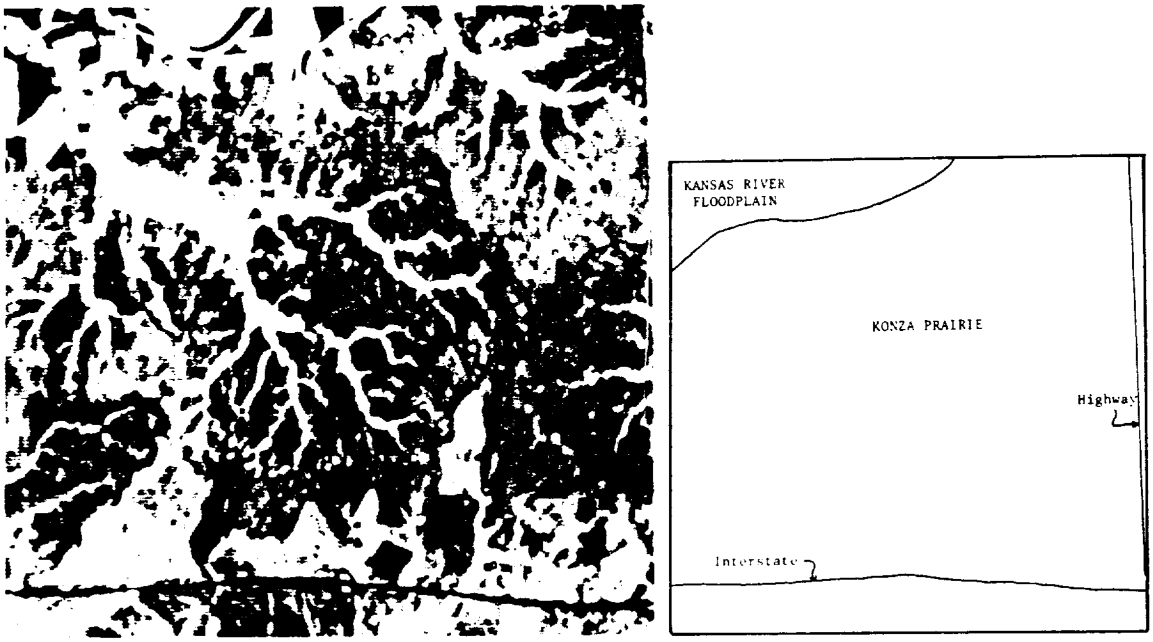

FIG. 3. SPOT HRV Normalized Vegetation Difference Indice of the Konza Prairie Research Natural Area on 01 May 1987.

Fourteen landscape areas (Table 1) indicative of land-use practices in the Flint Hill regions were selected to monitor seasonal changes. Because these areas were co-registered, it was possible to obtain spectral readings on the same geographical area from each geometrically corrected scene.

TABLE 1. LANDSCAPE AREAS MONITORED OVER THE GROWING SEASON

2D – Ungrazed area, biennial burned since 1977, last burned in 1986
1D – Ungrazed area, annually burned since 1977, last burned in 1987
UB – Long-term ungrazed, unburned not burned for 15 years
10 – Ungrazed area, burned every 10 years, last burned in 1981
4B – Ungrazed area, burned every 4 years, last burned in 1986
C1 – Long-term ungrazed, unburned for 7 years
PO – Grazed by domestic cattle, not burned in 1987
WH – Grazed by domestic cattle, burned in 1987
KI – Mixture of forest and grassland
GA – Mixture of forest and grassland
SH – Mixture of forest and grassland
NA – Mixture of forest and grassland
FA – Winter wheat field in 1987
AG – Soybean field in 1987

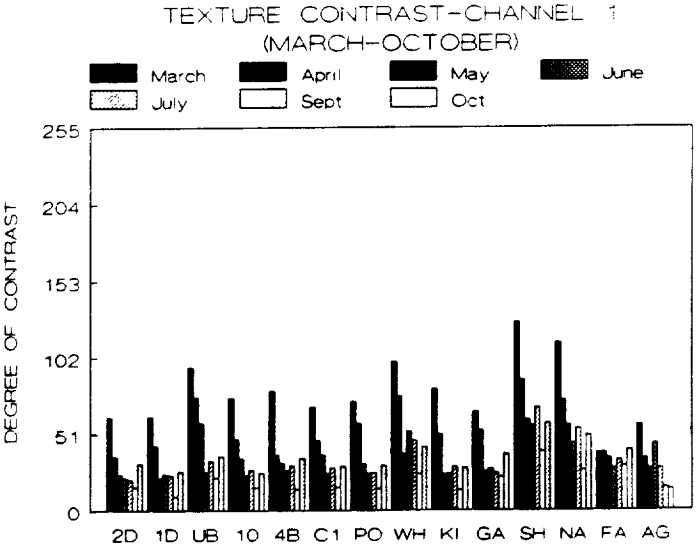

FIG. 4. Degree of Textural Contrast for channel 1 of the SPOT HRV satellite for the seven dates. Key for area is explained in Table 1.

RESULTS AND DISCUSSION

Heterogeneity (degree of landscape contrast), as determined by utilizing texture algorithms on channel one (0.50 to 0.59 micrometres), was higher (values ranging from 40 to 120) in the early part of the growing season for all landscape types (Figure 4). This early season contrast is probably due to variability present in the standing previous year's dead vegetation (i.e., between the standing vertical stems and mixed lodging of dead stems) and a lack of leaf cover in forest canopy allowing greater response from numerous understory components.

The measure of textural contrast, however, was most dramatic in the early season for riparian areas of mixed deciduous forest and native grassland (values from 40 to 120). As the soils warm and with reduced competition resulting from the late spring burns, C_4 grass (big bluestem, little bluestem, and Indian grass) production increases dramatically, thereby reducing the degree of heterogeneity in the areas with more frequent burning (i.e., watersheds 1D and 2D). In addition, in the riparian areas, trees leaf out in late April-early May. The result is a relatively rapid decrease in textural contrast, which may be due to more uniform canopies of trees and grasses obscuring the landscape diversity in the lower understory (down to a textural values of approximately 40). As variability in senescence begins to dominate in late summer and early fall, the degree of heterogeneity increases as measured by the textural algorithm (e.g., watershed 2D and 4B; Figure 4).

The lowest degree of seasonal variability in textural contrast was obtained for a winter wheat field/fallow field (Figure 4). The uniformity of the wheat stand in the early spring and same uniformity after harvest in stubble and mulch is reflected in the consistent low textural values (values of textural contrast of about 40).

In channel 2 (red wavelength band), the pattern of textural response across landscape units (Figure 5) is very similar to that for channel 1. The primary difference is the stronger vegetation response due to chlorophyll absorption in the 0.61 to 0.68 micrometre range. The result of this greater sensitivity is a higher level of textural variability (an increase of 10 to 20 percent) in landscape response (based on a higher degree of difference noted in the SPOT data for vegetative vigor in the spring) along with a more accurate level of textural reduction with senescence in the fall.

In channel 3 (the near IR), the pattern (Figure 6) is quite different from that for Channels 1 and 2. For most landform units, the June SPOT data provided the highest measure of textural values. This high level of heterogeneity is probably due to two strongly related factors: high precipitation and active plant growth during the June period (Figure 1). Abrams *et al.* (1986) summarized ten years of aboveground biomass data and climatic variables on Konza. Growing season precipitation was the most important variable associated with the aboveground biomass. June has the highest average amount of precipitation (16 percent of the total annual rainfall (Bark, 1987)). The high sensitivity of the near infrared to vegetation response and the subtlety of canopy structure can be detected with the textural algorithm. The seasonal variation in senescence intensity is also elaborated with channel 3 textural values.

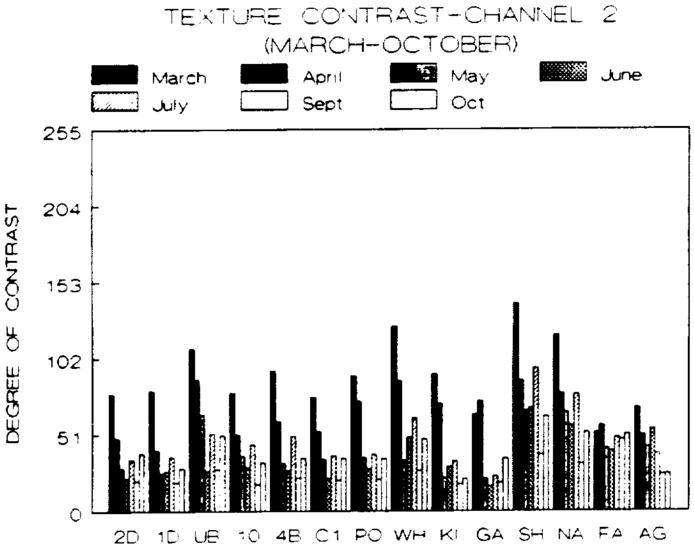

FIG. 5. Degree of Textural Contrast for channel 2 of the SPOT HRV satellite for the seven dates. Key for area is explained in Table 1.

Applying the textural algorithm to the NDVI, the textural pattern (Figure 7) is very similar to that for channel 3. The primary difference, however, relates to a consistently higher textural value for the NDVI data relative to the channel 3 data. This is most probably due to the greater sensitivity of the NDVI values to greenness and net primary productivity over that of channel 3 alone. Once again, the peak period of textural heterogeneity in most landscapes occurred in June and July (Figure 7). Highest textural values (greater than 200) were generated in the mixed forest/grasslands units. Watersheds left unburned for extended periods of time (8 years or more – e.g., UB; Figure 7) had moderate textural response values, but consistently higher than regularly burned watersheds (2D and 1D). The textural values highlighted the contrast between burned and unburned watersheds. The higher textural contrast values for unburned watersheds is probably due to a greater amount of tree cover (primarily eastern redcedars (*Juniperus virginiana*) and American elms (*Ulmus americana*)) mixed with woody shrubs (i.e., summacs (*Rhus aromatica*) and buckbrush (*Symphoricarpos orbiculatus*)) all mixed with native tallgrass prairie grasses.

CONCLUSIONS

Limited empirical information exists documenting the impact of landscape treatments (e.g., fire and grazing) on landscape diversity across a temporal time scale. A texture algorithm, when applied to individual SPOT channel data sets, and NDVI provide a quantitative approach to assist in understanding landscape heterogeneity in the tallgrass prairie ecosystem. Each channel provided some measured response in landscape contrast to changes in plant vigor and higher primary productivity.

It appears that a texture algorithm applied to either channel 3 or NDVI produced from the SPOT HRV digital data is most applicable to tallgrass prairie to detect various management treatments. The most significant amount of contrast was detected using channel 3 or the NDVI (Figures 6 and 7) although

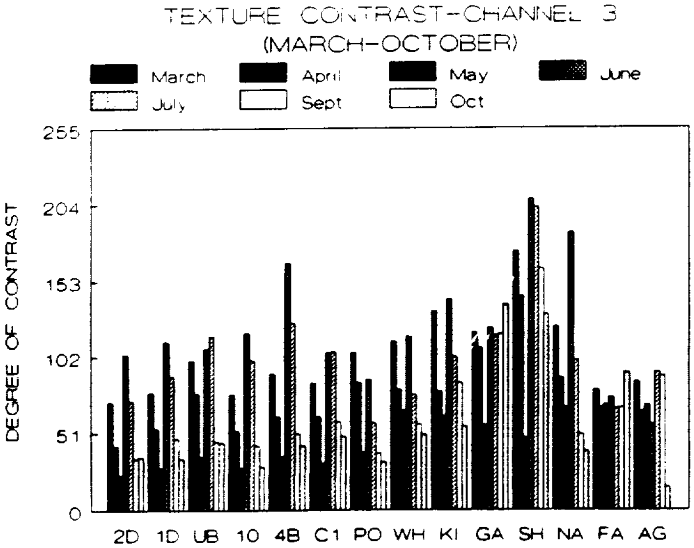

FIG. 6. Degree of Textural Contrast for channel 3 of the SPOT HRV satellite for the seven dates. Key for area is explained in Table 1.

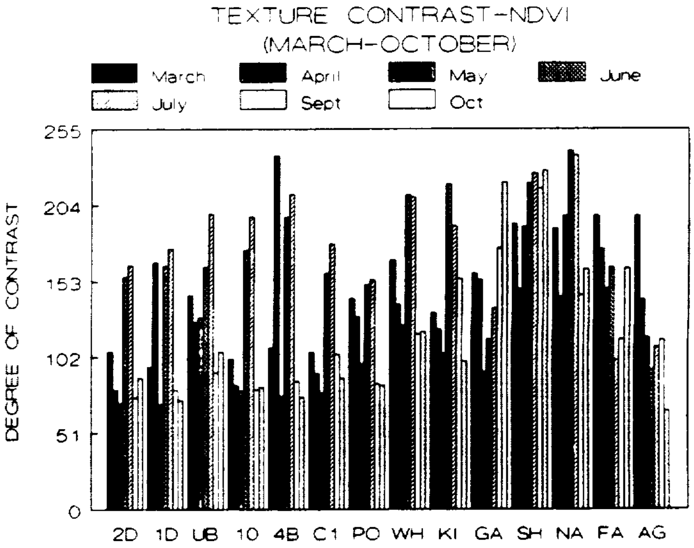

FIG. 7. Degree of Textural Contrast for NDVI generated scenes of the SPOT HRV satellite for the seven dates. Key for area is explained in Table 1.

NDVI contrast values were generally greater between areas of different management treatments. In addition, the texture algorithm applied to SPOT HRV derived NDVI values supported Collins and Gibson's work (in press) that annual burning reduces the diversity of tallgrass prairie landscapes. Both 1D and 2D (an annual and biennial burned watershed) had consistently lower values than the watersheds burned every four years or left unburned (Figure 7), suggesting that these areas had lower landscape heterogeneity (i.e., lower species diversity). Those areas which have been grazed by cattle (i.e., PO and WH) had similar texture values to those areas left unburned, even though WH was burned and PO was not burned, suggesting that grazing increases the landscape heterogeneity. Collins (1987) found that burning and grazing had significant effects on the invariant structure of the tallgrass prairie and Senft *et al.* (1987) reported that cattle grazing in shortgrass prairie also affected species diversity. These results suggest that textural algorithms applied to SPOT HRV derived NDVI can detect changes in vegetation communities induced by either fire or grazing.

The texture algorithm applied to SPOT HRV derived NDVI allowed detection of areas with the highest amount of landscape heterogeneity; the narrow bands of gallery forest surrounded by tallgrass prairie (Figures 4 to 7). These areas contain an eastern deciduous forest community intermingled with the tallgrass prairie ecosystem (Freemen and Hulbert, 1985; Freemen and Gibson, 1987).

Landscape ecology must consider new measures of heterogeneity in order to detect different landscape treatments and/or effects (Wiens, 1989). Remote sensing, coupled with textural algorithms, offers empirical confirmation to document treatment responses (both burning frequency and grazing) in a temporal framework for understanding landscape diversity in the complicated tallgrass ecosystem.

ACKNOWLEDGMENT

Support for this research was supported by NSF grant #85-14327. Konza Prairie Research Natural Area, a preserve of the Nature Conservancy, is operated by the Division of Biology, Kansas State University. The authors wish to thank the SPOT corporation for providing the original data input as part of the FIFE investigation.

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(Received 16 October 1989; revised and accepted 17 July 1990)

Reprinted from the Proceedings of the Eleventh North American Prairie Conference, T. Bragg and J. Stubbendieck (editors). University of Nebraska Printing, Lincoln, NE. 1989. 293 pages.

EFFECTS OF MANIPULATION ON FOLIAGE CHARACTERISTICS OF *ANDROPOGON GERARDII* VITMAN

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Abstract. The effects of burning, mowing, and nitrogen fertilizer on the chlorophyll, nitrogen, and phosphorus content of big bluestem were measured using a factorial experimental design at Konza Prairie Research Natural Area. While spring burning usually increased foliage production, burning had no effect on mid-season chlorophyll or nitrogen concentrations. Chlorophyll concentrations were significantly increased by fertilizer and mowing treatments. Nitrogen concentrations of foliage were higher on fertilized and mowed plots. Mowing also increased phosphorus concentrations of foliage, but nitrogen fertilizer significantly reduced phosphorus concentrations. These results support other research indicating that: 1) nitrogen use efficiency (grams biomass produced per gram of foliage nitrogen) is higher on burned prairie, 2) removal of foliage by mowing results in more nutrient-rich regrowth, and 3) the amount of phosphorus available to big bluestem foliage is limited. The dilution of phosphorus caused by added nitrogen was a consequence of increased productivity on these plots and suggests phosphorus uptake in excess of requirements for maximum growth. The relationships between burning, mowing, and nitrogen on the spectral reflectance patterns of vegetation indicated that chlorophyll (or nitrogen) concentrations of foliage appeared to more strongly affect indices of greenness and plant vigor than did the amount of plant biomass.

Key Words. biomass, burning, mowing, big bluestem, *Andropogon gerardii*, chlorophyll, nitrogen, phosphorus, Kansas

INTRODUCTION

Publications on the factors controlling the productivity of tallgrass prairie are abundant (Knapp and Seastedt 1986, Ojima 1987, Hulbert 1988). Current scientific emphasis is directed at understanding spatial patterns of productivity in relation to topography, fire, and grazing. Interest is increasing in the use of remote sensing procedures in these efforts. Spectral reflectance patterns have been used to monitor seasonal patterns of productivity both within and among terrestrial ecosystems (Goward *et al.* 1985, Asrar *et al.* 1986). For this type of approach to be useful in tallgrass prairie, knowledge of burning, mowing, and grazing on plant spectral reflectance characteristics must be understood on a basis of both per unit of foliage and per unit of vegetation area. Plant physiology and morphology, in conjunction with the absolute amounts of living and dead foliage, will affect the spectral reflectance measurements (Sellers 1985, Waring *et al.* 1985).

This study evaluated the effects of burning, mowing and fertilizer on the chlorophyll, nitrogen, and phosphorus content of the dominant tallgrass species, big bluestem (*Andropogon gerardii* Vitman). These results are then related to the effects of the respective treatments on prairie productivity and the spectral reflectance properties of this vegetation.

STUDY SITE AND METHODS

Research was conducted on the Konza Prairie Research Natural Area in the Flint Hills region of northeastern Kansas. The study area consisted of 32 plots (100 m^2) that had been: 1) annually burned or unburned since 1985, 2) mowed and raked twice per growing season or unmowed since 1985, and 3) fertilized with 10 g/m^2 of nitrogen as ammonium nitrate (NH_4NO_3) or untreated. This experiment consisted of four replicates of eight combinations of burning, mowing, and fertilizer additions. Mowing was conducted in late May and in mid-July. Species composition of these plots is similar to that reported by Hulbert (1988). Big bluestem was the dominant grass, but indiangrass [*Sorghastrum nutans* (L.) Nash] was also abundant. Forbs, including several milkweeds (*Asclepias* spp.) and goldenrods (*Solidago* spp.), were also common, particularly in unmowed plots.

Samples of big bluestem foliage for chlorophyll and nutrient analyses were collected on 3 July 1987 and immediately placed in refrigerated bags and returned to the laboratory. Leaf sheaths were removed prior to measurements. Wet weights of these samples were obtained and samples were then frozen until other analyses were conducted. Quantitative samples for biomass estimates were obtained on 15 July by clipping 0.1 m^2 of vegetation from each plot. Biomass from mowed plots represented regrowth after one mowing while biomass from unmowed plots represented total foliage production.

Methods of both extraction and spectrophotometric analysis of chlorophyll were based on the Delaney technique as used by Knapp and Gilliam (1985). The leaves were taken from the freezer one at a time, thawed by warming gently between the palms, then cut into 1 cm pieces, and weighed on a Mettler balance to 0.01 g. Chlorophyll A, chlorophyll B, and beta carotene were then extracted using 85% acetone, sand, and calcium chloride ($CaCO_3$) with a foil-covered mortar in a pestle. The leaves were ground for 1-2 minutes with a Talboy blender. The ground tissue and acetone were poured into a foil- covered, graduated centrifuge tube, and diluted to 10 ml with acetone. Each sample was centrifuged for 5 minutes and allowed to settle for 1 hour before measured in wavelengths of 750, 663, 644, and 452 nm on a Beckmann DB-GT spectrophotometer (Robbelen 1957).

Nitrogen and phosphorus values for foliage samples were obtained by drying and grinding additional foliage, digesting this tissue with a micro-Kjeldahl method, and determining nitrogen and phosphorus colorimetrically on a Technicon Autoanalyzer.

Spectral reflectance measurements were concurrently obtained by personnel involved on the NASA-FIFE experiment (FIFE = First ISLSCP Field Experiment, ISLSCP = International Satellite Land Surface Climatology Project). The spectral measurements determined total amount of reflected light at specific wavelengths. Here, an index of "greenness" or Green Vegetation Index (GVI) (Kauth and Thomas 1976) based on a linear combination of reflectances of various wavelengths, is used to describe the plots. Another index of plant vigor used to describe the plots, the normalized difference, is a ratio estimator created by subtracting red reflectance from the near-infrared reflectance and dividing this value by the sum of these reflectances (Goward *et al.* 1985).

Statistical analysis of these data employed a three-way ANOVA, using fire, mowing, and nitrogen as main effects. All possible interactions among the treatments were also evaluated. Due to the configuration of the plots, fire effects were tested using a block*fire interaction term. Other effects were evaluated with the error term.

RESULTS

An analysis of variance of nitrogen concentrations indicated no interactions among the main treatments of burning, mowing, and nitrogen additions. Nitrogen concentrations in foliage of big bluestem were higher in the fertilized plots than in control plots (Figure 1). Significantly higher nitrogen concentrations also occurred in mowed than in unmowed plots. Spring burning, however, did not significantly affect nitrogen concentrations (Figure 1).

An analysis of variance also indicated no interactions among the main treatment effects for phosphorus concentrations of foliage. Phosphorus increased in mowed plots at about the same ratio as the increase in nitrogen (Figure 2). In contrast, phosphorus significantly decreased in plots where nitrogen fertilizer was added (Figure 2).

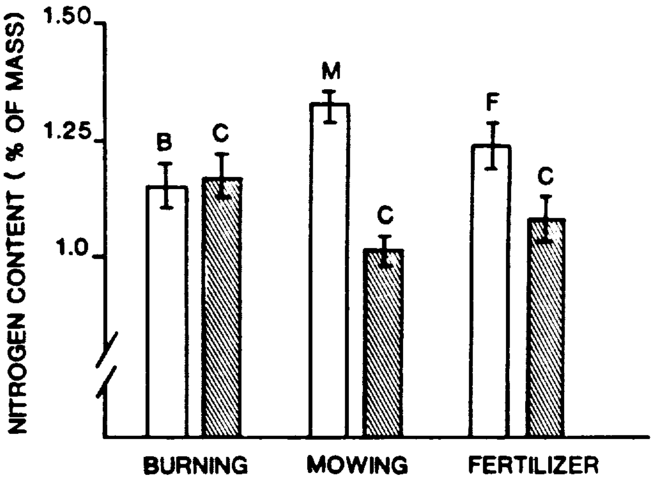

FIG. 1. Nitrogen concentrations of big bluestem foliage. Controls (C), represented by hatched bars, are compared to burned (B) plots, mowed (M) plots, or fertilized (F) plots. Error bars represent one standard error for 16 replicates.

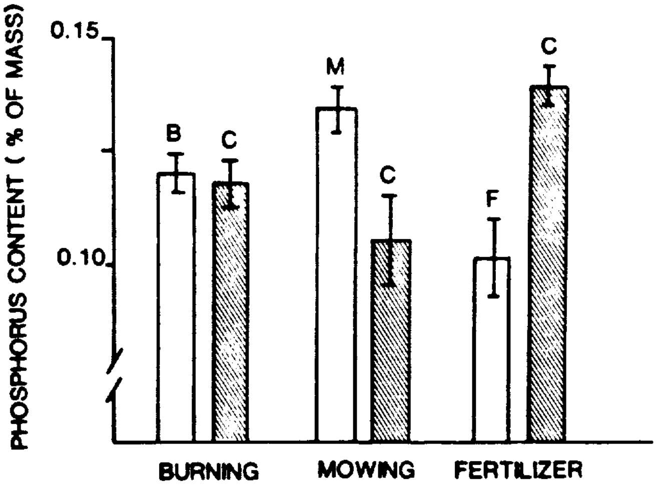

FIG. 2. Phosphorus concentrations of big bluestem foliage. Symbols are same as those used in Figure 1.

Fertilization with ammonium nitrate resulted in higher chlorophyll A and total pigment concentrations in big bluestem foliage (Figures 3 and 4). Mowing also significantly increased pigment concentrations while spring burning had no effect. An analysis of variance indicated modest ($p = 0.05$) interactions between mowing and fertilizer additions (for chlorophyll A concentrations) and for mowing and burning (for total pigment concentrations). Unmowed, unfertilized vegetation had lower chlorophyll A concentrations than mowed, unfertilized vegetation. Concentrations of chlorophyll A were similar for mowed or unmowed but fertilized vegetation. Burning tended to increase pigment concentrations on unmowed sites, but, it decreased concentrations on mowed sites.

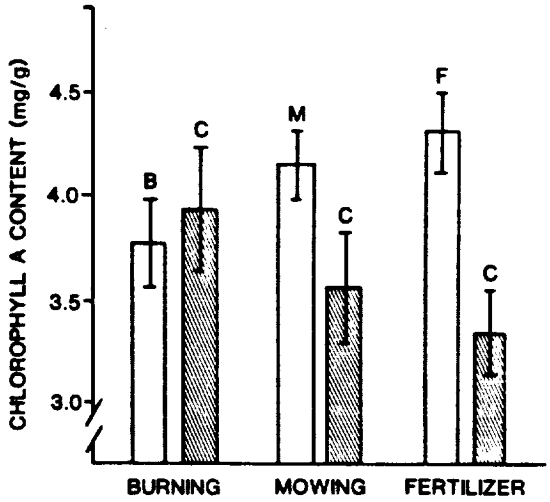

FIG. 3. Chlorophyll A concentrations of big bluestem foliage. Symbols are same as those used in Figure 1.

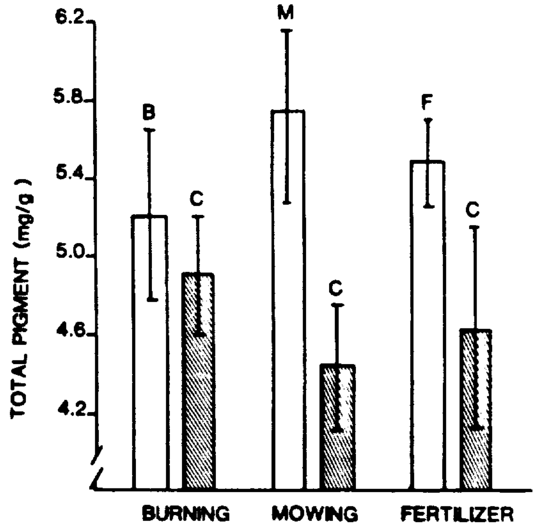

FIG. 4. Total pigment (chlorophyll A, chlorophyll B, and beta carotenes) of big bluestem foliage. Symbols are same as those used in Figure 1.

Plant biomass on the various plots was harvested on 15 July (Figure 5). Regrowth after mowing in late May on mowed plots was much greater on fertilized than on unfertilized plots. Overall, these midseason values show a strong mowing and fertilizer effect, and a non-significant effect of spring burning on plant biomass. Indices of plant greenness and plant vigor associated with this biomass are shown in Figures 6 and 7. When these values are compared with plant biomass (Figure 5), "greenness" appears to be more closely associated with nitrogen additions than with biomass. An analysis of variance of the reflectance-derived values indicated that all treatments except mowing and all two-way interactions among treatments were statistically significant. However, the amount of variance attributed to fertilizer was much more significant than any other variable or combination of treatments.

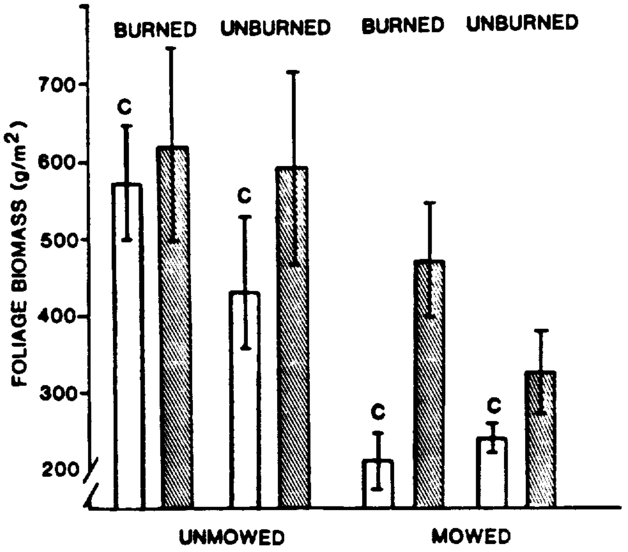

FIG. 5. Midseason foliage biomass on burned, mowed, and fertilized plots. Hatched bars represent the fertilized plots within each mowing and burning treatments.

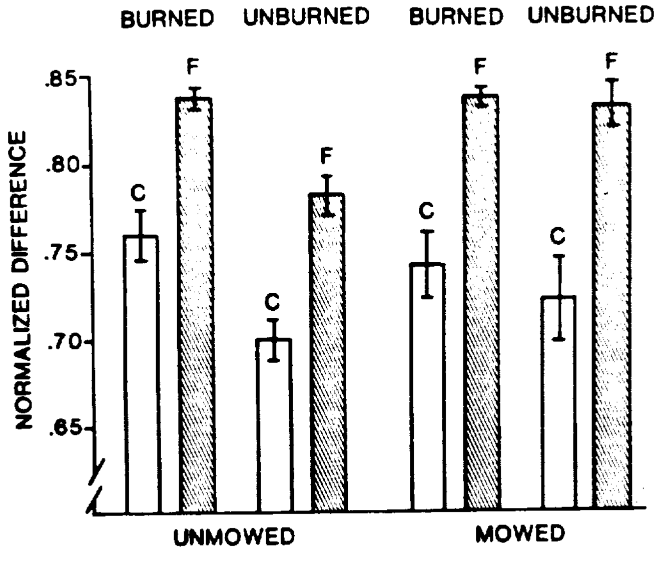

FIG. 6. Normalized difference, another index of plant vigor, for burned, mowed, and fertilized plots. Symbols are the same as those used in Figure 5.

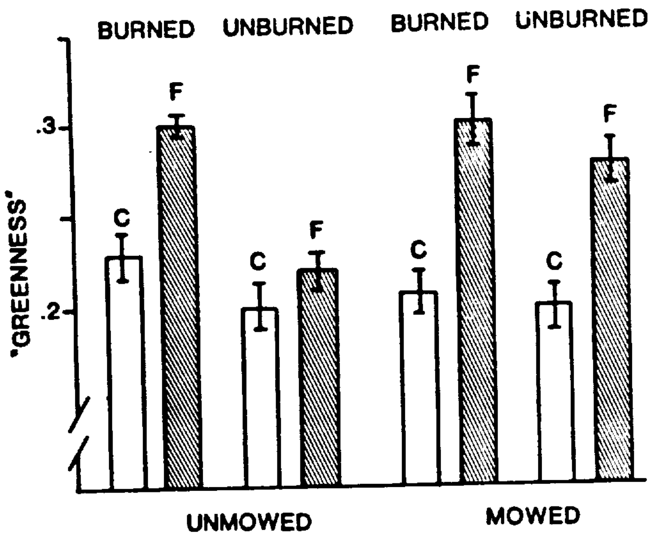

FIG. 7. "Greenness" in relation to burning, mowing, and fertilizer treatments. Controls (C), are compared to fertilized plots (F) within each mowing and burning treatment. Bars are one standard error for 8 replicates.

DISCUSSION

Midseason chlorophyll concentrations measured here for big bluestem are, on average, somewhat higher than values reported by other investigators (Bray 1960, Ovington and Lawrence 1967, Old 1969, Knapp and Gilliam 1985). These higher values reported in this study may reflect differences in methodologies rather than actual species differences or differences attributed to site effects. The age of the foliage at the time the chlorophyll measurements were made is important, although Ovington and Lawrence (1967) found little seasonal dynamics in concentrations of total chlorophyll in a Minnesota prairie.

Spring burning did not affect midseason chlorophyll or nitrogen concentrations. While the seasonality of nitrogen content of burned and unburned vegetation may differ markedly (Owensby *et al.* 1970), the overall amount of nitrogen available to vegetation on burned sites is not markedly different from unburned sites, and may in fact be less on burned sites (Ojima 1987). This implies that the increased productivity observed on burned sites in most years corresponds to increased nitrogen use efficiency by this vegetation.

Old (1969) measured the effects of nitrogen addition on midseason chlorophyll content and reported about a 20% increase in chlorophyll, a relative difference similar to that found in this study (Figure 3). This increase appears to be linearly related to the nitrogen content of this tissue. In contrast, phosphorus concentrations were not related to chlorophyll concentrations. While mowing increased chlorophyll, nitrogen, and phosphorus concentrations, addition of ammonium nitrate increased chlorophyll and nitrogen concentrations, but decreased phosphorus content. These data therefore suggest that big bluestem will accumulate phosphorus in concentrations higher than those limiting growth. Therefore, these plants exhibit luxury uptake of this element relative to nitrogen and/or other elements.

These results indicate that "greenness" as measured with the normalized difference procedure was sensitive to both burning and chlorophyll (nitrogen) content of the vegetation. The former treatment, which in this study did not significantly affect nitrogen concentrations, removed standing dead plant materials and litter and, thereby, changed the reflectance properties of the soil surface. Fertilization and mowing strongly affected nitrogen and chlorophyll concentrations. The reduction in biomass resulting from mowing may negate the positive effect that mowing had on chlorophyll and nitrogen content, such that measurements of greenness after a certain period of regrowth on mowed plots did not show a strong mowing effect. Other studies have suggested that canopy reflectance was sensitive to the physiological status of the plant at the time of measurement (Sellers 1985). This work tends to support this concept in that plots with reduced biomass but enhanced nitrogen content tended to have equal or greater indices of greenness than unmowed but unfertilized vegetation (Figure 7). These findings have important implications to studies on assessment of plant productivity or vegetation interactions with the atmosphere by remote sensing methods. Models using only foliage biomass or leaf area are unlikely to provide accurate estimates of either subsequent productivity or water-gas interactions.

ACKNOWLEDGEMENTS

This research was supported by NASA (NAG-5-897) and NSF (BSR-8514327) grants to Kansas State University. T. Dawn Shapley's current address is University of Kansas Medical Center, Kansas City, Kansas 66103.

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SPOT Satellite Data for Pattern Recognition on the North American Tall-Grass Prairie Long-Term Ecological Research Site

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Background to the Imaged Area

The Konza Tallgrass Prairie, a part of the Kansas Flint Hills, represents one of 15 research sites in the United States supported by the National Science Foundation for Long-Term Ecological Research (LTER) (Figure 1). The goal of the LTER program is to investigate a variety of features that characterize specific ecosystems – such as tropical savanna, eastern deciduous forest, and tallgrass prairie. Initial convergence of the LTER effort was encouraged by requiring that sites address research efforts in five core areas. These were (1) pattern and control of primary production; (2) spatial and temporal distribution of populations selected to represent trophic structure; (3) pattern and control of organic matter accumulation in surface layers and sediments; (4) pattern of inorganic inputs and movement of nutrients through soils, groundwater, and surface waters; and, (5) pattern and frequency of disturbance to the research site (Brenneman and Blinn, 1987).

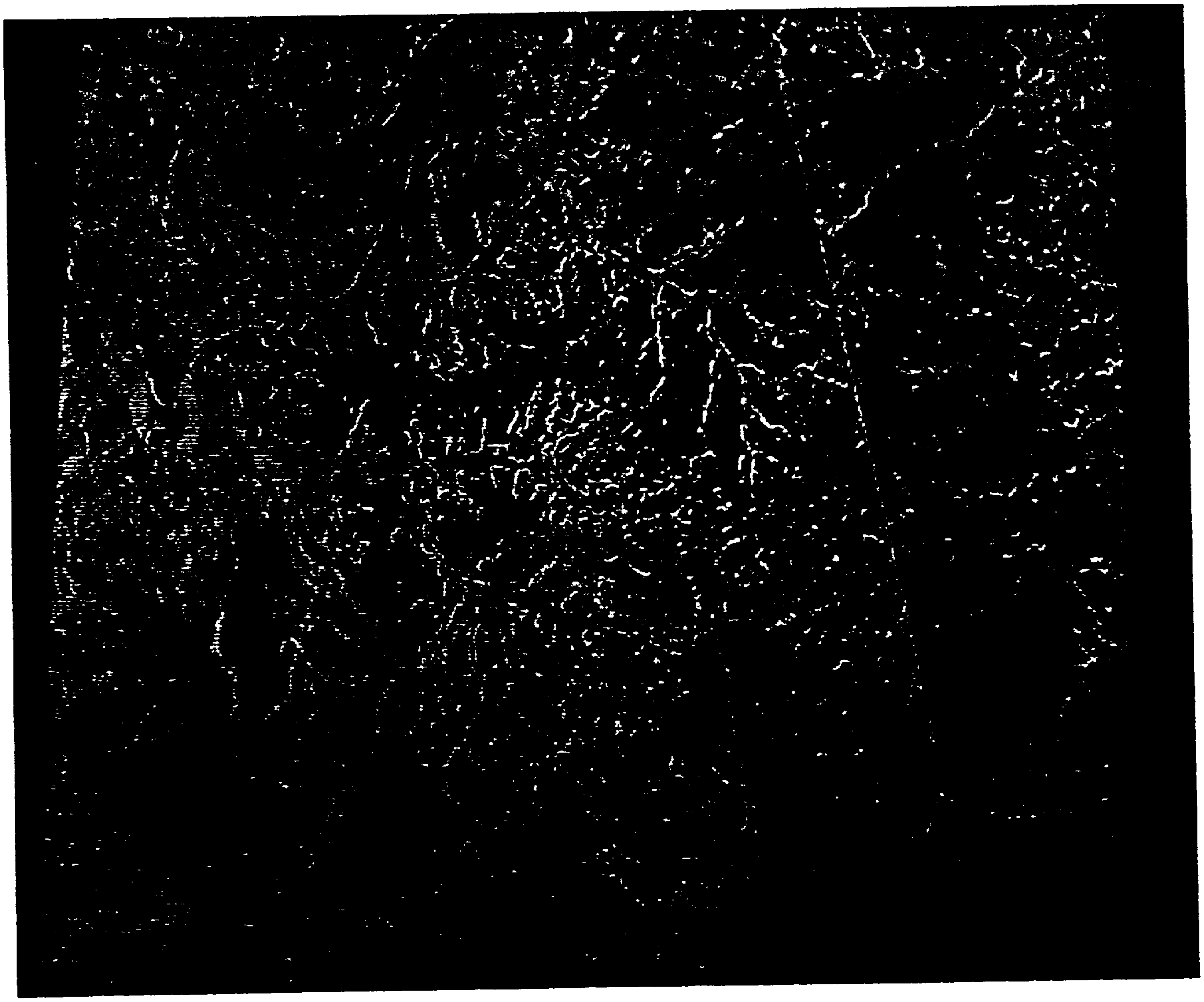
Slightly over a century ago, the tallgrass prairie in North America extended from what is now southern Canada to Oklahoma in the United States (Reichman, 1987). Today only a small fraction of the original tallgrass prairie remains; primarily in the Kansas Flint Hills (Figure 2). The Konza Prairie Research Natural Area, a 3,500 hectare protected tract, represents a portion of the original prairie established to preserve this vanishing habitat and to promote scientific research. The management objectives of the research area are based on understanding the impact of periodic fire, drought, and grazing on a tallgrass prairie ecosystem. Remote sensing and geographic information systems (GIS) technologies provide important methods for studying the Konza Prairie and for LTER intersite comparisons.

Analytical Procedures and Conclusions

Figure 3 was generated using an unsupervised classification cluster routine on digital data collected by SPOT satellite on May 1, 1987. The cluster routine uses a two-pass sequential clustering algorithm. In the first pass, the program reads through the entire data set, and sequentially builds clusters (groups of points in spectral space) based on parameters selected by the user, and computes the mean value for each cluster. These clusters become the signatures used to assign classes in the output G.I.S. file.

The second pass classifies each pixel in the data set according to a minimum distance classifier. The algorithm calculates the spectral distance between the candidate pixel and the mean value for every cluster, using the mean values that were computed in the first pass. The class with the minimum or shortest spectral distance (ERDAS, 1988). Processing of the SPOT data was performed on a micro-based ERDAS integrated image processing system. For the May scene of Konza Prairie, the unsupervised cluster routine classified the tallgrass prairie area into 11 classes (Figure 4). The classes represent variations in rural land use from intensive cropland agriculture systems (where wheat, corn, sorghum, and soybeans are primary crops) to extensive grazing systems. The approach allowed for detailed mapping of variations in watershed treatment based on frequency of burning and grazing systems. Annually burned watersheds were easily distinguished from less frequently burned watersheds. As the tallgrass prairie is left unburned, the proportion of C4 species declines (e.g. big and little bluestem *(Andropogon geradrii and Andropogon scoparius)*, switchgrass *(Panicum virgatum)*, and indiangrass *(Sorghastrum nutans)*. At the same time these same watersheds increase in forbs and woody species.

Fig. 1 The network of Long-Term Ecological Research Sites includes 15 sites that range from arctic and alpine tundra to grasslands. New sites added in 1987 are represented by a * (Brenneman, et al., 1987)



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Acknowledgement

This research was funded through National Science Foundation Grant # BSR 85-14327. The authors also wish to thank SPOT IMAGE CORPORATION for providing the original data input as part of the FIFE investigation.

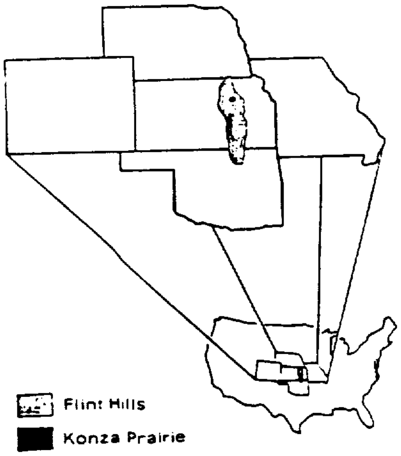
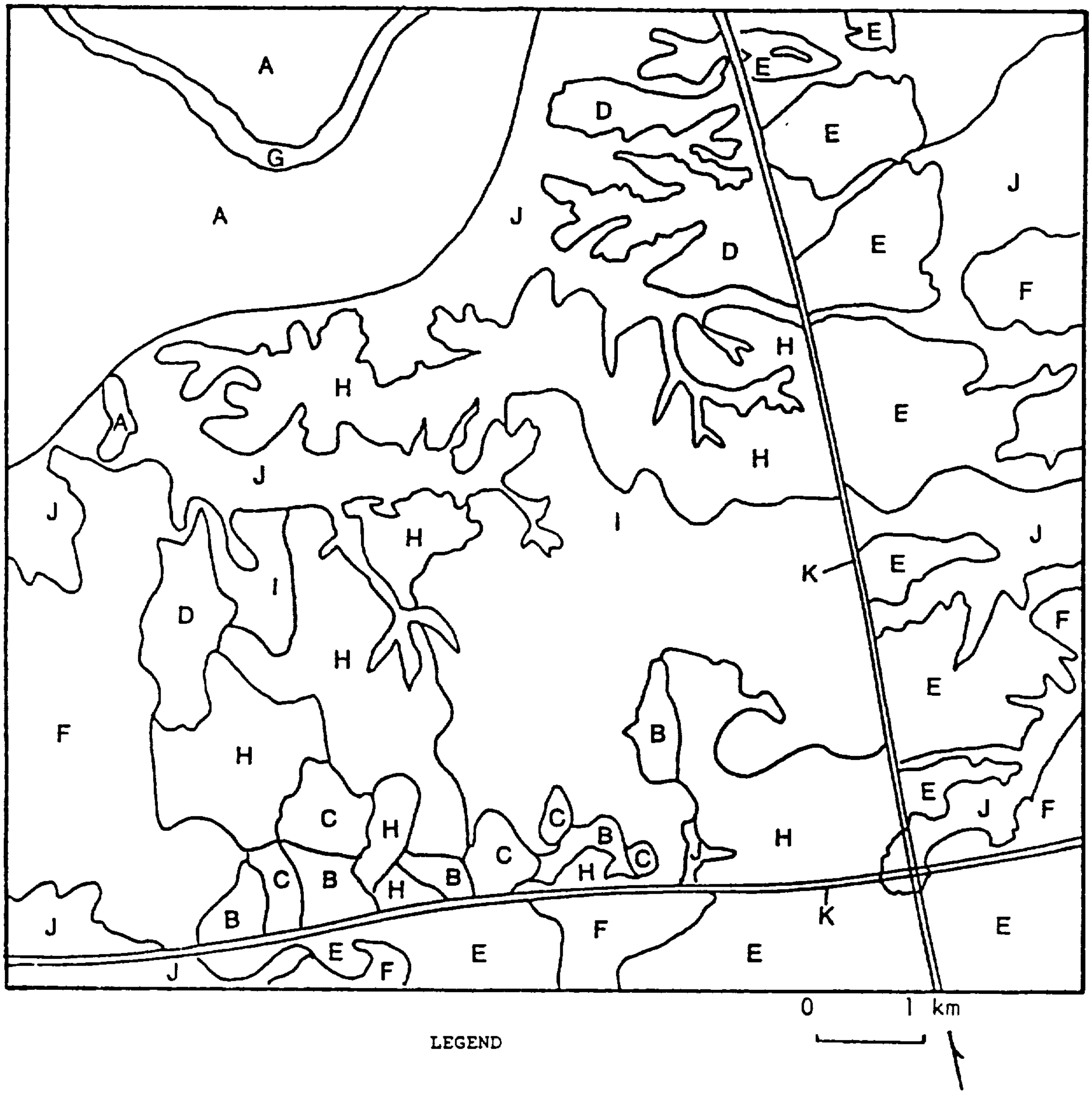


Fig. 2 The Konza Research Natural Area within the Kansas Flint Hills.

Fig.4 Major classes of land cover resulting from the unsupervised classification.



LEGEND

A--Agriculture (Cropped and Fallow) and Alluvial Floodplain

B--Ungrazed Tallgrass Prairie Burned At Least Two Consecutive Years

C--Ungrazed Tallgrass Prairie Burned During Current Year (But not Previous Year)

D--Most Recent Ungrazed Prairie Burned During Current Year

E--Grazed Tallgrass Prairie Burned During Current Year

F--Grazed Tallgrass Prairie and Unburned During Current Year

G--Kansas River

H--Ungrazed and Short-term (Less than 4 years) Unburned Tallgrass Prairie

I--Ungrazed and Long-term (Greater than 4 years) Unburned Tallgrass Prairie

J--Riparian Forest (Eastern Deciduous)

K--Highway