

Seasonal, topographic and burn frequency effects on biophysical/ spectral reflectance relationships in tallgrass prairie

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Abstract. Application of remote sensing relies on understanding how the physical properties of surfaces (especially vegetated surfaces) control spectral reflectance. Empirical investigation of links between canopy properties/processes and spectral response have generally consisted of univariate modelling of one spectral response variable in terms of one canopy property, or less frequently, in terms of two or more canopy variables. While this approach has been fruitful, it cannot account for multivariate interactions of spectral and surface properties in determining canopy response across the spectrum. In this study, two closely related multivariate analysis techniques, canonical correlation and redundancy analysis, are used to investigate the relationship between a series of tallgrass prairie canopy biophysical properties and spectral reflectance measured *in situ* using a portable radiometer. To capture a variety of different conditions within the tallgrass canopy, data were collected at two times during the 2002 growing season (28 May and 18 August), from two different slope/aspect situations, located on one frequently burned and one infrequently burned watershed. Results suggest that canopy structure (canopy height, greenness fraction) is the most consistent influence on spectral reflectance during both data collection periods. Canopy optical properties also emerge as an important control in August. Neither soil moisture nor plant physiology/biochemistry systematically influenced spectral reflectance. The relative importance of the various canopy variables shows some dependence on burn frequency and topographic setting.

1. Introduction

Applications of remote sensing can generally be divided into two domains: (1) retrieval of biophysical information, and (2) classification of land use/land cover (Jensen 1983). Although these two application domains are often considered independently of one another, they have many elements in common. Each is based on interpretation of spectral reflectance, but in each domain it is not spectral reflectance *per se* that is of interest, but physical or thematic information embedded within (and retrievable from) the spectral data. Also, in each application domain, some sort of model or algorithm is used to convert spectral reflectance data into

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some form of biophysical or thematic information. Thus, spectral reflectance data are proxies for useful information about various aspects of the Earth's surface. Understanding how such information (whether thematic or biophysical) is extracted from spectral data is the foundation of remote sensing science.

Retrieval of biophysical information from remote sensor data is generally done using correlative or model-derived relationships between biophysical variables and spectral data in the form of in-band spectral reflectance (Ahlriches and Bauer 1983, Curran 1983, Maas 1998) or a vegetation index derived from spectral reflectance (Shibayama and Akiyama 1989, Christensen and Goudriaan 1993, Price and Bausch 1995, Gilbert *et al.* 1996, Carlson and Ripley 1997, White *et al.* 2000). Generally, these empirical or modelled relationships between spectral and biophysical information are univariate. A single dependent biophysical variable is predicted from a single independent spectral variable. Studies of the multivariate relationships between canopy properties and spectral response are rare compared to those detailing univariate relationships. Wiegand *et al.* (1992) examined the effect of various canopy properties on the spectral reflectance of wheat. Jakubauskas (1996) examined the relationships between Landsat Thematic Mapper (TM) bands and canopy structural/biotic variables for coniferous forest cover in Yellowstone National Park, USA, using canonical correlation analysis. Sampson *et al.* (2001) used canonical redundancy analysis, a multivariate approach based on canonical correlation, to examine the relationship between spatial structure and spectral response in hardwood forest. Cohen *et al.* (2003) described an improved strategy for extracting biophysical information from Enhanced Thematic Mapper (ETM)+ images of coniferous forest using multivariate techniques. These studies have shown that multivariate relationships between canopy properties and spectral response are complex and scale dependent; characterized by multidimensional, intercorrelated relationships among both the spectral and biophysical variables (Korobov and Railyan 1993). Multivariate analysis of the relationship between canopy biophysical properties and spectral response can contribute to both application domains in remote sensing, by revealing the composite effects of canopy properties on reflectance and by informing the physical interpretation of thematic classes defined by multispectral classification.

In this study, multivariate analysis techniques are used to examine the relationships between canopy and spectral variables in tallgrass prairie. Understanding these relationships is important in tallgrass prairie because the canopy is spectrally dynamic in space and time (Davidson and Csillag 2003) and shows spatial-spectral structure at very fine scales (Goodin and Henebry 1998). Tallgrass prairie is noteworthy for the importance of fire and fine-scale topographic variability as agents of ecological variability (Collins and Wallace 1990, Knapp *et al.* 1998). This study was designed to capture the effect of seasonality, topographic position and fire frequency on the multivariate relationship between canopy biophysics and spectral response.

2. Methods

2.1. *The study area*

Data were collected at the Konza Prairie Biological Station (KPBS; 39° 08' N, 97° 58' W) located 12 km south of Manhattan, Kansas, USA (see figure 1). The study site is located within the Flint Hills, a narrow band of conical, stream-dissected hills characterized by local relief varying from 50–100 m, extending latitudinally across eastern Kansas from near the Nebraska border into Oklahoma.

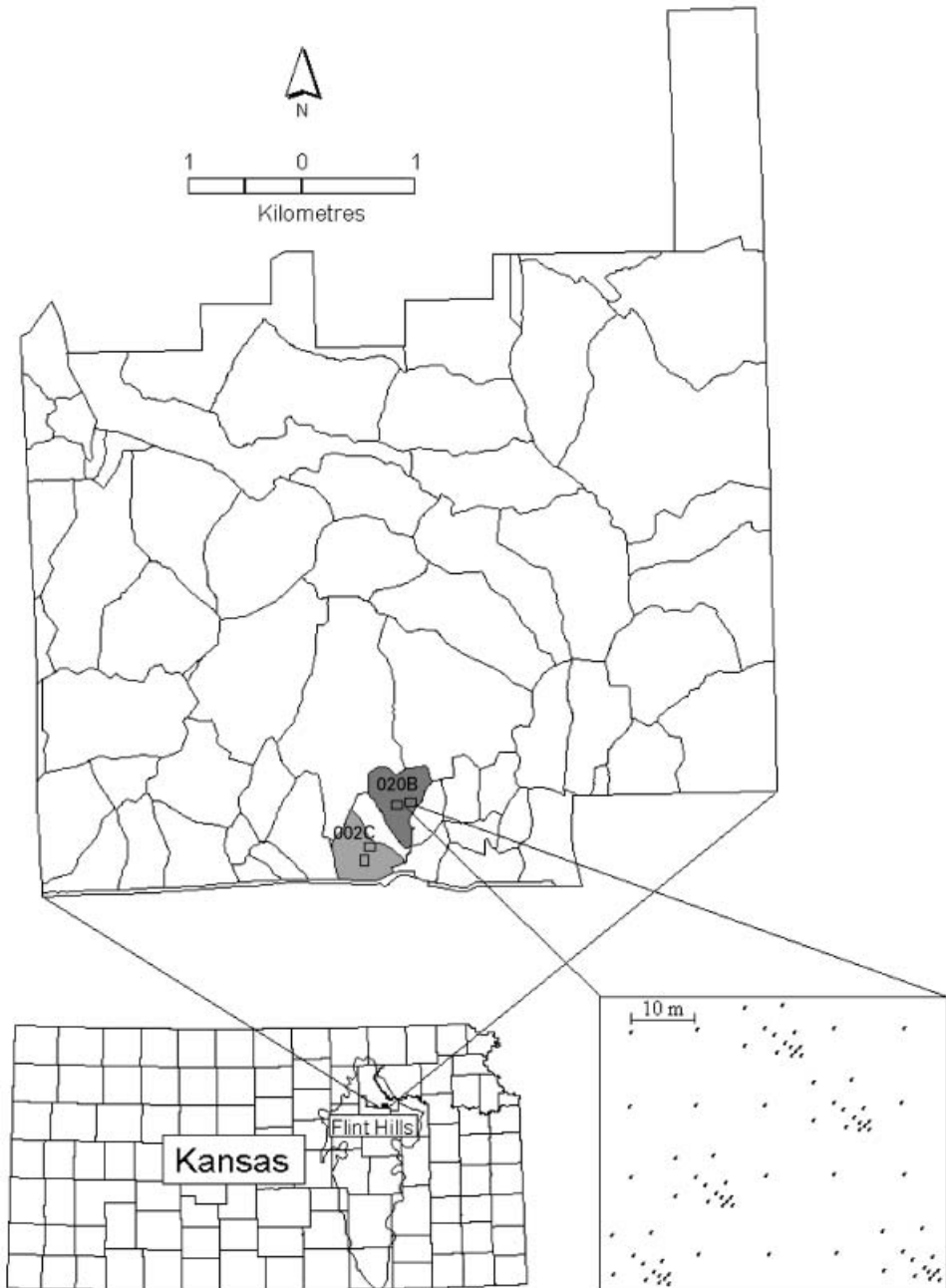


Figure 1. Location of KPBS, showing the watersheds where data were collected. Rectangles within the shaded watershed indicate location of sampling grid. Layout of the sampling grid is shown in the inset.

The Flint Hills are the largest contiguous remnant of the North American tallgrass prairie (Risser *et al.* 1981). Research at KPBS focuses on the long-term effects of fire, grazing and climate on tallgrass prairie structure, function and dynamics (Knapp and Seastedt 1998). Konza occupies 3487 ha, divided into 60 experimental

watersheds, each permanently assigned to a grazing treatment (grazed by cattle, grazed by bison, or ungrazed) and a prescribed burn frequency (1, 2, 4, 10 or 20 year fire return interval). Graminoid plant species dominate, with the majority of phytomass composed of *Andropogon gerardii* (Big Bluestem), *Schizochyrium scoparius* (Little Bluestem), *Sorghastrum nutans* (Indiangrass) and *Panicum virgatum* (Switchgrass), with *Bouteloua gracilis* (Blue Grama), *B. curtipendula* (Sideoats Grama) and *Buchloe dactyloides* (Buffalograss) occurring in drier areas. Forbs and woody species are subdominant, although present in greater variety and thus accounting for more species richness (Collins and Glenn 1991, Hartnett and Fay 1998). Common forbs include members of the *Solidago*, *Aster*, *Artemisia* and *Ambrosia* genera. Woody vegetation of the genera *Rhus*, *Amorpha* and *Cornus* occur where fire frequency is low (Freeman 1998).

2.2. Field data collection

Data were collected during two field campaigns; one conducted on 28 May 2002, the other on 18 August 2002. These dates were selected to capture contrasting stages in the development of the tallgrass prairie canopy. In spring (represented by the May dataset) soil moisture is generally sufficient due to accumulation of moisture during the prior dormant period. Solar radiation is the key limiting resource. By mid summer (represented by the August data), the canopy has reached peak greenness and begun to yellow. Evapotranspiration has depleted much of the stored soil moisture, thus canopy water stress is generally greater than in the early growing season. During each field campaign, data were collected from two watersheds with contrasting burn frequencies. One of these watersheds (002C) is burned on a two-year cycle and was last burned in April 2000. The other watershed (020B) is a long-term unburned unit, last burned in 1986. These two treatment types were chosen to represent extremes within the range of naturally occurring tallgrass prairie communities (Knapp and Seastedt 1998). More frequent burning homogenizes the prairie canopy by removing accumulated litter, suppressing invasion of woody species, and favouring the growth of a variety of C₃ forbs within a matrix of C₄ graminoids (Collins and Wallace 1990). As burn frequency decreases, the prairie canopy becomes more heterogeneous as a larger variety of forbs, graminoids and woody species become established. Thus, watershed 020B was characterized by substantial growth of woody trees and shrubs, whereas vegetated cover in 002C consisted mainly of dominant graminoids with subdominant forbs. Differences in the two watersheds are illustrated by contrasts in summary descriptive statistics (see table 1).

To capture topographic variability, two sampling grids were established on each watershed. On watershed 002C, grids were established on adjacent east- (slope 24°, aspect 84°) and south-facing (slope 20°, aspect 177°) slopes. On 020B, the grids faced east (slope 26°, aspect 96°) and west (slope 28°, aspect 267°). Selection of measurement sites with multiple fire treatment and topographic conditions, combined with sampling from two distinct stages of canopy phenology, allowed us to compare the effect of canopy variables on spectral reflectance under a variety of representative conditions.

Data were collected from 40 m × 50 m grids with 60 sampling points arranged in a nested pattern (see figure 1). Spectral reflectance was measured using a Cropscan MSR-5 field-portable spectroradiometer. Spectral sensitivity of the MSR-5 emulates bands 1–5 of the Landsat TM. The MSR-5 instrument consists of two sets of

Table 1. Statistical summary of the data. Format is: mean (SD). All dates are 2002.

Variable	Watershed 020B				Watershed 002C			
	29 May		16 August		29 May		16 August	
	East	West	East	West	East	South	East	South
R _{grn}	11.6 (1.4)	10.2 (1.4)	10.2 (1.6)	8.64 (1.8)	10.7 (1.4)	10.6 (0.8)	11.1 (1.1)	10.6 (1.0)
R _{red}	10.8 (2.2)	7.9 (2.3)	9.8 (2.0)	7.34 (2.2)	9.6 (1.9)	9.8 (1.8)	9.6 (1.2)	10.4 (1.2)
R _{nir}	46.1 (4.0)	49.8 (8.6)	49.3 (6.1)	47.3 (9.2)	43.9 (3.5)	41.4 (5.4)	49.7 (6.6)	44.4 (4.1)
R _{mir}	63.9 (8.7)	53.3 (8.1)	58.1 (9.4)	50.7 (8.6)	54.3 (5.4)	53.0 (4.4)	56.7 (5.8)	58.9 (3.7)
NDVI	0.62 (0.1)	0.72 (0.1)	0.67 (0.1)	0.73 (0.1)	0.64 (0.1)	0.61 (0.1)	0.67 (0.0)	0.62 (0.0)
Chl	32.0 (4.0)	32.4 (4.7)	32.4 (5.3)	35.0 (4.7)	30.0 (2.3)	29.4 (2.7)	27.0 (2.9)	24.6 (3.2)
HT	34.8 (38.4)	46.8 (44.1)	51.2 (43.8)	61.1 (41.6)	28.8 (7.6)	28.8 (7.6)	31.5 (9.6)	40.1 (8.2)
PWC	0.77 (0.1)	0.73 (0.1)	0.58 (0.1)	0.55 (0.1)	0.69 (0.1)	0.68 (0.1)	0.52 (0.1)	0.53 (0.1)
F _{par}	0.35 (0.2)	0.34 (0.2)	0.25 (0.1)	0.20 (0.1)	0.15 (0.2)	0.24 (0.2)	0.10 (0.0)	0.21 (0.1)
VWC	36.4 (17.3)	30.0 (11.9)	27.9 (14.3)	25.7 (10.6)	56.7 (21.5)	76.3 (29.8)	60.6 (17.4)	53.1 (15.9)
F _{grn}	0.70 (0.2)	0.63 (0.3)	0.66 (0.1)	0.49 (0.1)	0.71 (0.1)	0.63 (0.1)	0.67 (0.1)	0.68 (0.1)
%N	2.62 (5.3)	2.53 (5.3)	1.37 (0.2)	1.32 (0.2)	1.30 (0.3)	1.25 (0.3)	1.06 (0.2)	1.05 (0.1)
%C	42.2 (2.4)	42.9 (3.6)	45.1 (1.0)	45.8 (1.4)	43.2 (1.2)	43.1 (0.7)	44.9 (0.9)	44.9 (0.8)
C:N	23.0 (5.0)	24.2 (5.1)	33.8 (5.1)	35.4 (4.8)	34.9 (7.2)	36.7 (9.1)	43.1 (6.0)	43.6 (5.5)

matched sensors, one set pointed upward and covered with an opal glass diffuser to collect irradiance, the other pointed downward toward the target with a 28° instantaneous field of view (IFOV). The MSR-5 simultaneously collects data from each set of sensors, computes the ratio between them in real time and applies solar zenith angle corrections to determine reflectance. Due to a persistent malfunction, band 1 (0.45–0.52 μm) was not used in this analysis. The radiometer was suspended over each measurement site on a hand-held aluminium mast ≈ 1.5 m above the soil surface (the minimum height possible with this apparatus). At this height, the sensor's 28° field of view yields a circular target with an IFOV of $\approx 0.4\text{ m}^2$. Spectral data were collected between 1000 and 1400 LST (time zone GMT-6) to minimize the effect of varying solar illumination angle (Milton 1987). Normalized Difference Vegetation Index (NDVI)—derived from spectral reflectance data—is used extensively for estimating canopy biophysical properties (Malingreau 1989, Baret and Guyot 1991), and was therefore calculated from red reflectance (R_{red}) and near-infrared reflectance (R_{nir}) and used in this analysis.

Concurrently with the spectral data, a canopy biophysical dataset was collected consisting of nine variables: leaf chlorophyll content (Chl), canopy height (HT), leaf percentage water content (PWC), fraction of absorbed photosynthetically active radiation (F_{par}), volumetric soil water content (VWC), fraction of green vegetation cover (F_{grn}), foliar nitrogen content (%N), foliar carbon content (%C) and carbon–nitrogen ratio (C:N). Each of these variables was measured from the area within the IFOV of the multispectral radiometer and within 2 h of spectral data collection. Leaf chlorophyll content (Chl) was measured using a Minolta SPAD-502 meter (Loh *et al.* 2000). Five samples were taken within the spectrometer IFOV and averaged to yield Chl values. Soil moisture was measured using a portable time domain reflectometer (TDR) probe (Spectrum Technologies, TDR-300). A line Photosynthetically Active Radiation (PAR) ceptometer with a 1 m probe (Delta-T devices, Sunscan) was used to measure F_{par} . Vegetation cover fraction (F_{grn}) was calculated from colour digital photographs taken vertically at 1.5 m above the canopy (Rundquist 2001). Vegetation canopy height (HT) was measured using the visual obstruction method (Robel *et al.* 1970). Canopy PWC, %C, %N and C:N ratio were calculated from 10 g grass samples collected along with the other canopy data and temporarily stored in sealed airtight polyethylene ('zip-lock') bags for subsequent analysis. These samples were weighed, oven dried for 24 h at 80°C, then reweighed to determine PWC (fresh sample weights were determined within 2 h of initial collection, samples were kept on ice until weighed). Nitrogen and carbon percentage were determined from the oven-dried samples by combustion chromatography (Carlo-Erba NA-1500 element analyser). Carbon–nitrogen ratio was calculated from %C and %N.

The biophysical variables selected for the study represent a number of biotic and abiotic characteristics known to affect canopy spectral response. Among the biotic characteristics, HT and F_{grn} are bulk structural properties, representing the density and growth form of the canopy. Other biotic variables are more related to individual plant physiology (PWC, Chl) and biochemistry (%C, %N and C:N) (Asner 1998). Fraction of absorbed photosynthetically active radiation (F_{par}) is a biotic variable that quantifies both optical and structural properties of the vegetation canopy. Soil volumetric water content, the sole abiotic variable used in the analysis, was included because it affects turgidity/vigour and is an important limiting factor for plant growth.

2.3. Data analysis

Multivariate relationships between spectral and biophysical canopy variables were evaluated using canonical correlation (CCA) and redundancy analysis (RDA). These two techniques are computationally similar; both are members of the class of general linear multivariate analysis techniques that also includes principal components analysis, canonical variate analysis, and multivariate regression (ter Braak 1995). In both CCA and RDA, groups of two or more variables are related to one another by simultaneous extraction of linear components from both sets of variables so that the correlations between the linear components are maximized (van den Wollenberg 1977). In canonical correlation, the two sets of variables, called canonical variates (CVs) are allowed to enter the calculation symmetrically, thus no predictive relationships emerge from the analysis (ter Braak 1990). Canonical correlation is useful for exploring the multivariate correlation structure of a dataset, and is capable of revealing latent correlation structures not apparent from standard univariate linear correlation analysis (Thompson 1984).

Redundancy analysis also finds correlated linear combinations of groups of input variables, but differs from CCA in that the relationship between the variable groups is assumed to be asymmetric. That is, one set of variables are considered dependent response variables, the other set are assumed to be predictors of the first set. The linear combinations of predictor variables are called redundancy factors, and each redundancy factor accounts for a known proportion of the variance in the response variables. The redundancy of each variable is the mean squared loading of one set of variables on the canonical variates of the other set (van den Wollenberg 1977), thus the link between CCA and RDA. Redundancy values correspond to the principal components of the variables computed from the covariance matrix of the linear regression of the dependent variables on the independent variables, thus RDA can also be considered a canonical form of PCA (Goovaerts 1994, ter Braak 1995). All multivariate analyses were done using the SAS/STAT software, version 8 (SAS Institute 1999).

3. Results and discussion

3.1. Results from canonical correlation

Following the suggestion of ter Braak (1990), results of CCA are presented as bivariate plots with canonical variates as axes (figures 2 and 3). In this format, the correlation structure of the data is revealed graphically. Only the first two CVs were significant (see tables 2 and 3), thus only bivariate plots of CV1 and CV2 are presented. The distance between the variable and the CVs in canonical space shows the strength of correlation of variables with the two CVs. Similarly, correlated canopy and spectral variables plot near one another in canonical space. Negatively correlated variables plot in opposite quadrants of the bivariate plot, with the distance between them proportional to the strength of the negative relationships. Weakly correlated variables plot in adjoining quadrants. To clarify the interrelationships between canopy and spectral variables, the spectral variables in the bivariate plots are shown as arrows emanating from the origin, while the canopy biophysical variables appear as points.

Examination of the biplots for each combination of observation date, burn treatment type, and slope/aspect combination shows some persistent relationships between the various spectral variables (figures 2 and 3). For all eight combinations of slope/aspect, date and fire treatment, the arrows representing R_{grn} , R_{red} and R_{mir} point in roughly the opposite direction from that of NDVI, indicating a strong

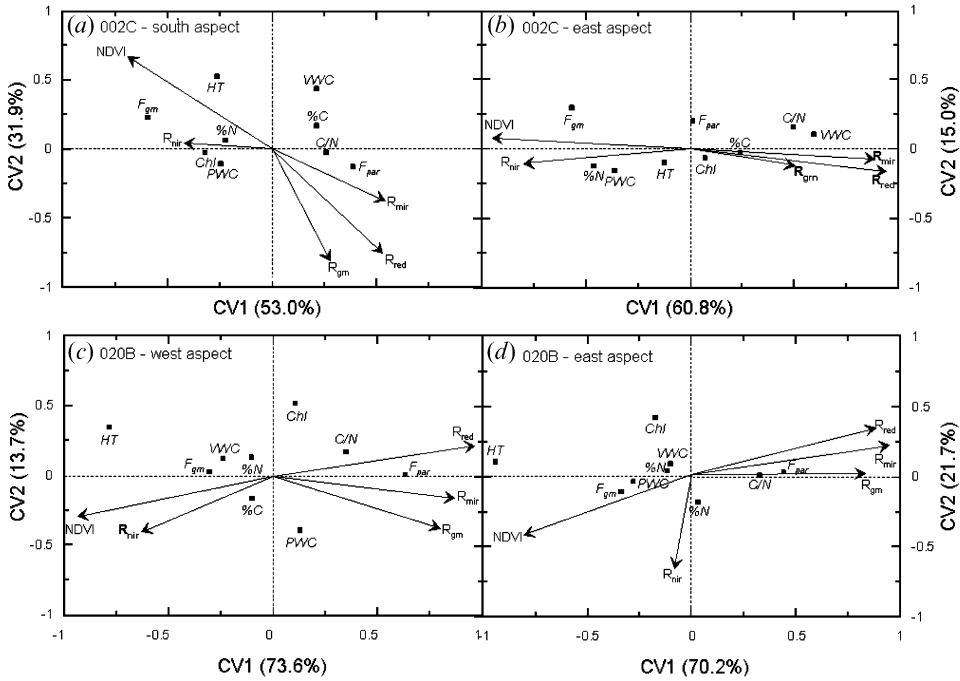


Figure 2. Canonical bivariate plots for 28 May 2002 dataset. Plotted values are correlations between the spectral and canopy variables and the first two (significant) canonical variates. Spectral variables are indicated by arrows, canopy variables by square symbols. Parenthetical numbers on axis labels indicate the percentage of total variance accounted for by that canonical variate.

negative correlation between these variables in canonical variate space. The negative correlation between R_{red} and NDVI is consistently strong across all treatment combinations. For these vegetated surfaces, biophysical interpretation of this pattern of negative correlation makes sense, since denser vegetation (hence higher NDVI) is associated with increased chlorophyll absorption in the red region of the spectrum (Knipling 1970, Gausman 1977).

In contrast, the R_{nir} arrow points in the same general direction as NDVI, indicating a positive correlation on all four canonical bivariate plots. In watershed 002C, the correlation between R_{nir} and NDVI tends to be strongest (i.e. both have high negative values on CV1) on the east-facing slopes, especially in the May data. The NDVI and R_{nir} are less correlated on the south-facing slopes, with the relationship weakest in the August data (figure 2(b)). On watershed 020B, R_{nir} is also most strongly related to NDVI on the west-facing slope in the May data (figure 2(c)). In the August data (figure 3(c) and 3(d)), R_{nir} was weakly correlated with each canonical variate, indicating that it has little influence on NDVI values. The persistent strong negative correlation between R_{red} and NDVI, coupled with the positive but weak relationship between NDVI and R_{nir} , suggests that much of the variation of NDVI in these data can be attributed to variation in red reflectance. Red reflectance in 020B in August was higher than it was in 002C because of the greater exposure of litter, bare soil, and rock in the unburned watershed. The lesser influence of R_{nir} in determining variability of NDVI was unexpected, in light of the well-documented prominence of the near-infrared region

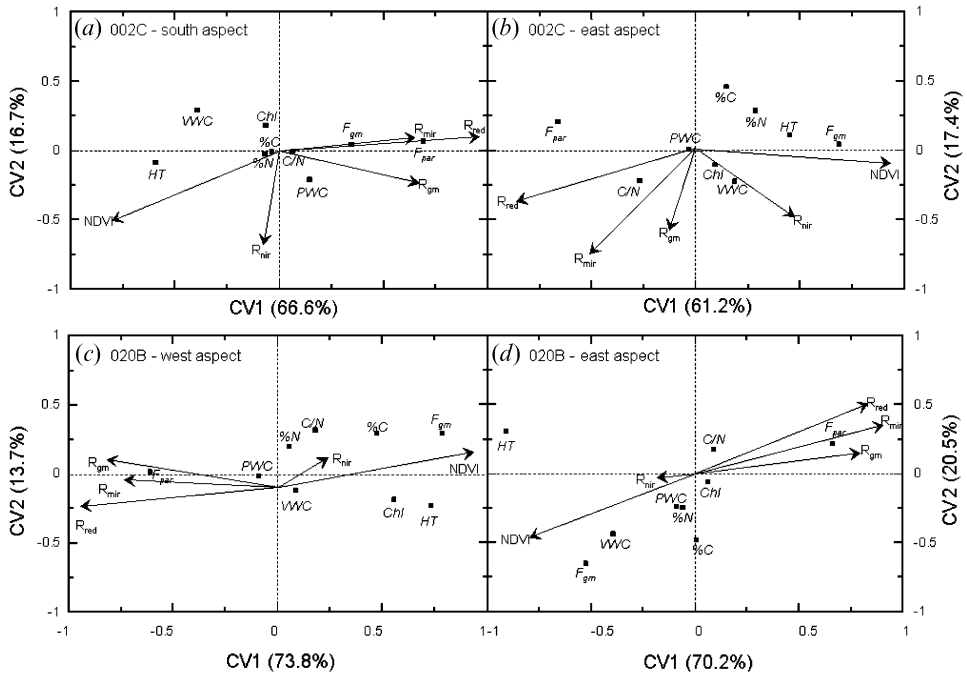


Figure 3. Canonical bivariate plots for 18 August 2002 dataset. See caption of figure 2 for detailed explanation of plot.

Table 2. RDA results for watershed 020B and 002C on 28 May 2002. Independent spectral variables are shown in normal typeface. Dependent canopy variables are shown in italics. Table entries are the squared multiple correlations between each variable and the first three canonical variates. The redundancy value represents the normalized percentage or variance explained by each canonical variate.

Variable	Watershed 020B				Watershed 002C			
	East aspect		West aspect		South aspect		East aspect	
	CV1	CV2	CV1	CV2	CV1	CV2	CV1	CV2
<i>R_{grn}</i>	0.48	0.48	0.53	0.61	0.40	0.04	0.14	0.15
<i>R_{red}</i>	0.53	0.57	0.77	0.80	0.38	0.15	0.53	0.54
<i>R_{nir}</i>	0.00	0.19	0.32	0.41	0.10	0.10	0.40	0.40
<i>R_{mir}</i>	0.61	0.63	0.62	0.63	0.21	0.15	0.47	0.48
NDVI	0.44	0.52	0.71	0.76	0.47	0.27	0.56	0.56
<i>Chl</i>	0.02	0.10	0.02	0.27	0.10	0.10	0.01	0.01
<i>HT</i>	0.61	0.61	0.61	0.72	0.35	0.07	0.01	0.02
<i>PWC</i>	0.05	0.05	0.02	0.18	0.07	0.06	0.13	0.15
<i>F_{par}</i>	0.14	0.14	0.41	0.41	0.17	0.15	0.00	0.04
<i>VWC</i>	0.01	0.01	0.05	0.07	0.24	0.05	0.36	0.37
<i>F_{grn}</i>	0.08	0.08	0.09	0.09	0.41	0.36	0.32	0.41
<i>%N</i>	0.01	0.01	0.01	0.02	0.05	0.05	0.21	0.23
<i>%C</i>	0.00	0.02	0.01	0.04	0.08	0.05	0.06	0.06
<i>C:N</i>	0.08	0.08	0.12	0.15	0.07	0.07	0.25	0.28
<i>p</i> -value	<0.01	0.02	<0.01	<0.01	<0.01	0.05	<0.01	0.03
Canonical <i>R</i> ²	0.69	0.44	0.85	0.60	0.58	0.45	0.63	0.29
Redundancy	0.41	0.07	0.58	0.05	0.33	0.25	0.67	0.06

Table 3. RDA results for watersheds 020B and 002C on 18 August 2002. Independent spectral variables are shown in normal typeface. Dependent canopy variables are in italics. Table entries are the squared multiple correlations between each variable and the first three canonical variates. The redundancy value represents the normalized percentage of variance explained by each canonical variate.

Variable	Watershed 020B				Watershed 002C			
	East aspect		West aspect		South aspect		East aspect	
	CV1	CV2	CV1	CV2	CV1	CV2	CV1	CV2
R_{grn}	0.48	0.49	0.55	0.57	0.01	0.12	0.27	0.28
R_{red}	0.52	0.64	0.74	0.75	0.48	0.52	0.55	0.55
R_{nir}	0.03	0.03	0.04	0.06	0.14	0.22	0.00	0.13
R_{mir}	0.62	0.68	0.45	0.45	0.17	0.36	0.25	0.25
NDVI	0.48	0.58	0.71	0.73	0.56	0.57	0.39	0.46
<i>Chl</i>	0.00	0.00	0.30	0.33	0.01	0.02	0.00	0.04
<i>HT</i>	0.63	0.68	0.52	0.58	0.20	0.21	0.35	0.36
<i>PWC</i>	0.01	0.03	0.01	0.01	0.00	0.00	0.02	0.06
F_{par}	0.34	0.36	0.39	0.39	0.45	0.49	0.48	0.49
<i>VWC</i>	0.12	0.21	0.03	0.13	0.03	0.08	0.15	0.24
F_{grn}	0.21	0.41	0.60	0.69	0.46	0.47	0.12	0.12
$\%N$	0.00	0.03	0.01	0.02	0.08	0.16	0.00	0.00
$\%C$	0.00	0.11	0.21	0.30	0.02	0.24	0.00	0.00
<i>C:N</i>	0.01	0.02	0.00	0.04	0.08	0.12	0.00	0.00
<i>p</i> -value	<0.01	0.01	<0.01	<0.01	<0.01	0.04	<0.01	0.02
Canonical R^2	0.76	0.48	0.82	0.46	0.65	0.34	0.60	0.27
Redundancy	0.43	0.06	0.49	0.06	0.27	0.09	0.17	0.07

in the spectral reflectance curve of green vegetation (Knipling 1970, Gausman 1977). Previous studies similar to ours (e.g. Wiegand *et al.* 1992, Korobov and Railyan 1993, Jakubauskas 1996) noted a much greater influence of R_{nir} on NDVI.

Since the biophysical canopy variables are the independent variables explaining the observed pattern of spectral reflectance, ideally there should be little or no intercorrelation among them. The distribution of biophysical variables in canonical variate space does indicate the presence of some correlation, but unlike the spectral variables, there is no indication of groups of variables persistently correlated across burn treatment type, data collection period or slope/aspect. There are some notable patterns of correlation within watersheds, however. In the May data, *C:N*, *VWC*, F_{par} and $\%C$ appear to be weakly correlated with one another on both the east- and south-facing grids of watershed 002C, based on their proximity in bivariate canonical space (figure 3(a) and 3(b)). Plant water content and $\%N$ also lie in close proximity to each other on both 002C grids. The observed relationship of these variables on both grids suggests that they may be linked biophysically. Clearly, *C:N* is related to $\%C$, but the ratio is also determined by $\%N$, which is not correlated to either variable. The potential explanatory link between canopy $\%N$ and *PWC* is also not readily apparent. Abundant N and available water contribute to canopy greenness, but the correlation between these two variables is not consistent across all treatments and grids in these data. On watershed 020B, F_{grn} , *VWC* and $\%N$ are correlated on both east- and west-facing grids, as are *C:N* and F_{par} . Again, the underlying biophysical linkages between these variables are not readily apparent. None of the other canopy variables are consistently correlated in the May dataset.

In the August data, there are fewer variables correlated on both grids compared

to the May data. On watershed 002C, only the two tissue nutrient content variables (%C and %N) occur together in canonical space on both grids. These variables are interrelated, in that both are indicative of canopy biochemistry. Note that the C:N ratio is correlated with %C and %N on the south-facing grid, but not on the east-facing one. No other variables are correlated on both grids. On watershed 020B, PWC and %N are correlated—the relationship is nearly perfect on the east-facing grid. These same two variables were correlated on both grids in the May 002C data; however, the reoccurrence of this relationship later in the season and on the contrasting burn treatment does little to clarify the relationship between them. The lack of consistent correlations between canopy biophysical variables across fire treatment, topographic setting or data collection period argues against any persistent underlying biophysical linkages between any of the canopy variables. The occasional correlations noted here should not necessarily be interpreted as thematic biophysical links.

3.2. Redundancy analysis

While CCA elucidates the multivariate correlation structure of the data, redundancy analysis provides a more rigorous analysis of the influence of the canopy variables on the spectral data. The results of RDA (tables 2 and 3) are interpreted using the squared multiple correlations between the various canonical variates and the spectral and canopy variables. These squared multiple correlations are similar to factor loadings in principal components analysis (ter Braak 1995). The redundancy values associated with each canonical variate quantify the normalized amount of data variance accounted for by that variate—an indicator of the ‘importance’ of each canonical variate and of the canopy and spectral variables correlated with that variate.

Redundancy analysis of the dataset reveals that, in every case, two significant canonical variates were extracted from the dataset. With the exception of the south grid in watershed 002C from the May data, the redundancy value for the first canonical variate accounted for an overwhelming proportion of the variance, indicating that CV2 had little power to predict the spectral variables. Because of the disparity in predictive power between the two canonical variates, in most instances it was only necessary to analyse the first canonical variate. The RDA results show some common relationships between canopy biophysical and spectral variables on all grids and across both dates; however, they also show some variations that appear to be due to topographic setting, fire treatment and canopy phenological state.

3.2.1. Redundancy analysis of May data

In the May dataset, redundancy values are similar for the first two canonical variates on the south-facing grid of 002C. This was the only grid where the redundancy of the first canonical variate was not substantially higher than the second (table 2). Although the redundancy for CV1 and CV2 are similar in value, the squared multiple correlations (hereafter referred to as ‘loadings’) are higher on canonical variate 1 (CV1), than on canonical variate 2 (CV2). High loading on CV1 by all spectral variables but R_{nir} suggests spectral reflectance across the spectrum is influenced by similar canopy properties. The low loadings for R_{nir} , coupled with the stronger loading of R_{red} and NDVI, supports the conclusion made in §3.1 that R_{red} is the reflectance component most responsible for variability in NDVI in these data.

Among the canopy biophysical variables, F_{grn} and HT appear to be the most important determinants of spectral reflectance. Both of these variables represent aspects of the physical structure of the canopy. Of the remaining canopy variables, only soil moisture (VWC) and F_{par} produced loading values exceeding single digits. VWC is probably linked to canopy height and density because greater root zone soil moisture facilitates soluble nutrient uptake, enabling vigorous canopy growth. F_{par} is influenced by the optical properties of the canopy (i.e. leaf transmissivity), but is also linked to canopy structure because a tall or denser canopy will absorb more PAR. The remaining canopy variables did not produce sufficiently high loading values to warrant further analysis.

On the east-facing slope of watershed 002C, CV1 accounts for 67% of the redundancy, far more than accounted for by CV2. As on the south-facing slopes, nearly all of the spectral variables are strongly correlated with CV1, the exception in this case being R_{grn} . Note that R_{nir} is well correlated with CV1 here, whereas it did not load strongly on either canonical variate on the south-facing slope. Among the canopy biophysical variables, F_{grn} and VWC most strongly influence the spectral variables (0.32 and 0.36 loadings on CV1, respectively). Unlike the south-facing slope, HT had almost no influence. The results from the east-facing grid also differ from those of the south-facing in that leaf biochemical variables (i.e. %N and the C:N ratio) load strongly.

Redundancy values for the May data from watershed 020B also indicate that the first canonical variate explains the majority of the variance in the data (table 2). On the east-facing slope, all of the spectral variables load relatively strongly on CV1 except for R_{nir} , which has a loading value of 0.0. On the west-facing slope, the loading for R_{nir} is higher, yet still considerably less than the other spectral variables. Once again, high loadings by R_{red} and NDVI, coupled with the lack of correlation with R_{nir} , suggest that red reflectance determines most of the variability in NDVI values. Middle infrared reflectance loads more strongly on CV1 in watershed 020B compared to CV1 in 002C. Since reflectance in the middle infrared is inversely correlated with water-bearing plant tissues, it is an important component of the overall spectral response from 'non-green' components of the canopy such as stems and litter (Gausman 1977). Because fire suppresses woody vegetation and removes litter from previous years' growth (Collins and Steinauer 1998), the importance of R_{mir} on watershed 020B (compared to 002C) is likely attributable to the absence of fire. Among the explanatory canopy biophysical variables, HT emerges as the most important on both grids. F_{par} loads strongly on CV1 on the west-facing grid, but less so on the east-facing grid.

3.2.2. Results and discussion of August redundancy analysis

As in the May data, the first canonical variate accounts for the majority of the redundancy in the August data (table 3), so that only CV1 need be analysed. On watershed 002C, 27% and 17% of the variance on the east- and south-facing slopes, respectively, is accounted for by CV1. Among the spectral variables, R_{red} and NDVI load strongest on CV1 on both the south and east aspects of 002C, whereas R_{nir} does not correlate strongly to any canonical variate. This supports the finding evident throughout this analysis that R_{red} is a more important determinant of variability in NDVI than R_{nir} . The rest of the spectral variables actually load more strongly on CV2, but since the second canonical variate accounts for only 9% of the variance on both the east- and south-facing slopes, it is unlikely that these loadings

indicate significant explanatory power. In fact, the overall low redundancy in the August data from watershed 002C suggests that much of the spectral variability on this watershed might be related to factors other than those measured in this study.

The pattern of loadings among the canopy biophysical variables on watershed 002C shows some similarity with the May data, but also some notable differences. In the May data, canopy structural variables (F_{grn} , HT) were the dominant controls on spectral variables. In the August data, F_{par} is now the strongest determinant of reflectance. As noted earlier, F_{par} is a canopy biophysical variable related to both the optical and structural properties of the canopy. It is also highly correlated to leaf area index in tallgrass prairie (Walter-Shea *et al.* 1992). The emergence of F_{par} as an important correlate with spectral response later in the season reflects the fact that the canopy is no longer actively growing and that its height is much more uniform than it was earlier in the season, especially compared to 020B (see SD values in table 1). Thus, the density and optical properties of the canopy are now more important, and their effect is manifest in the importance of F_{par} . Although less important than F_{par} , canopy structural variables are still important. Canopy height is less important than it was earlier in the growing season (due to the more uniform canopy height), but F_{grn} continues to load strongly on CV1, indicating that canopy density is now the more important structural determinant of reflectance.

On watershed 020B, CV1 accounts for 43% of the variance on the east-facing slope and 49% on the west-facing slope (table 3). All of the spectral variables for both aspects load strongly on CV1, except R_{nir} . By now, the pattern and implications of weak loadings associated with R_{nir} is familiar. Among the explanatory variables, canopy structure continues to be important. Canopy height exerts the strongest influence on spectral reflectance, just as it did in the May data. However, other canopy variables also load strongly on CV1. F_{grn} emerges as a strong explanatory variable on the west-facing slope, but a less important one on the east aspect. As in the May data, F_{par} continues to exert some influence on the canopy variables on the west-facing slope. However, its importance on the east-facing slope increased compared to the May data. We also note that %C shows modest importance on the west-facing slope.

4. Conclusions

In this study, we considered the relationships between spectral reflectance and canopy properties for one land cover type (tallgrass prairie), under a variety of treatment conditions, topographic settings and canopy phenological states. The significance of our findings lies in the conclusions drawn about the spatial and temporal relationships between canopy properties and spectral reflectance. In nearly every case, RDA showed that most of the spectral variables including NDVI loaded heavily onto the first canonical variate, which was the CV that accounted for the majority of variance in the data. This was more apparent in the May data than in the August data. Correlation of most spectral variables with the same CV indicates that the same biophysical properties (i.e. those canopy variables which also load strongly on CV1) are controlling reflectance across the spectrum. The single spectral variable that failed to correlate frequently with CV1 was R_{nir} , which, except for one instance, did not load heavily on any of the canonical variates. Given the prominence of R_{nir} in the reflectance spectrum of green vegetation (Knipling 1970, Gausman 1977) and its observed importance in previous multivariate studies of reflectance in forest (Jakubauskas 1996) and cropland (Wiegand *et al.* 1992, Sampson *et al.* 2001), its lack of importance here is noteworthy. The similarity of

correlative response among the other four spectral variables and the lack of importance of R_{nir} is surprising in light of the standard model for spectral reflectance from green vegetation. According to this standard model, visible reflectance should be controlled by leaf physiology (i.e. pigment content), near-infrared response by cell structure, and middle infrared response by tissue water content (Hoffer 1978). The standard model for vegetation reflectance was derived from laboratory measurements that concentrated only on leaf materials. However, our results suggest that spectral reflectance *in situ* responds to a much larger range of controlling factors, perhaps due to the wider variety of biotic and abiotic materials (e.g. soil, litter, stems) present in the IFOV of the instrument under field observation conditions. These findings might also mean that overactively growing grassland canopies, the high reflectance values and lack of dynamic range in R_{nir} contribute to the saturation effect frequently observed in NDVI values (Gitelson 2004). Further research incorporating modified, saturation-resistant forms of NDVI (Gitelson 2004, Viña *et al.* 2004) into multivariate analysis of canopy biophysical controls could yield insight into this problem. In addition, spectral data were obtained with a relatively coarse spectral resolution instrument—repeating this experiment with hyperspectral radiometry could reveal canopy reflectance responses that are correlated to other biophysical properties but too spectrally fine to be identified here.

Among the canopy biophysical variables, the two structural variables (HT and F_{grn}) were the most consistently correlated with CV1. In all of the eight measurement sets, one of these two variables was among the two strongest correlates with CV1, and in six of eight sets one of the two is the strongest correlate. Since the spectral variables (with the exception of R_{nir}) all loaded onto CV1, it can be concluded that throughout the growing season, canopy structure is the most consistent control over spectral reflectance. Structural factors are especially important earlier in the May dataset, when the canopy is still greening and developing.

By the time of the August data collection, the canopy has finished growing and was experiencing water stress. Canopy structure continues to be a dominant control on spectral reflectance—structural variables are the strongest correlates on both 020B grids and the south-facing grid on 002C. However, F_{par} (a variable encompassing both structural and optical canopy properties, see §2.2) also emerges as a consistent, strong influence on spectral response. This is especially apparent on watershed 002C, where the correlation of F_{par} with CV1 is strongest among all the canopy biophysical variables on the east-facing grid and nearly identical with F_{grn} on the south-facing grid. This suggests that canopy optical properties are more important in determining spectral response in the mature tallgrass canopy, relative to a canopy that is still growing and developing. Variables representing leaf physiology and soil moisture (%C, %N, C:N, Chl, PWC, VWC) appear as significant correlates occasionally, but their importance does not appear to be consistently or systematically linked to canopy phenology, fire treatment or topographic setting. At this relatively coarse level of spectral resolution, canopy structure and optics are the dominant physical controls on reflectance.

These findings shed light on biophysical interpretation of reflectance from tallgrass prairie (and perhaps grasslands in general) and contribute to both of the application domains of remote sensing discussed in §1. The lack of any consistent correlation between spectral reflectance and specific biophysical variables (e.g. F_{par} , HT, Chl, C:N, etc.) suggests that spectral reflectance and NDVI cannot be

univariately linked to any single biophysical property. Rather, our results indicate that canopy reflectance and NDVI are controlled by complex, multivariate interactions of canopy structure and optics. These results certainly do not contradict the use of spectral reflectance indices as univariate predictors for tallgrass canopy properties, especially canopy structural properties. However, this analysis suggests that researchers should be cautious about assuming that the biophysical relationships between canopy properties and spectral response in tallgrass prairie are spatially and temporally invariable, especially at fine spatial scales and over small spatial extent. These results show that canopy treatment history, topographic setting and phenological development state all affect the relationship between biophysical canopy properties and spectral response. Cohen *et al.* (2003) showed that multivariate analysis could be used to develop better regression models for predicting biophysical properties from spectral reflectance data. The results presented here support their conclusions by showing how the correlation between biophysical properties and spectral reflectance vary in response to time, treatment and topographical situation, and how CCA/RDA can be used to determine an optimal selection of spectral variables for predicting canopy properties.

These analyses can also help inform multispectral interpretation of tallgrass canopy spectral data, particularly with respect to classification into functional or ecological categories (Lobo 1997). Often, the goal of such classification is to segment an image into ecologically meaningful categories for further analysis or monitoring (Treitz *et al.* 1992, Lobo *et al.* 1998). Our results help interpret the biophysical meaning of these spatially segmented data.

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