Indicators of plant species richness in AVIRIS spectra of a mesic grassland

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Abstract

Hyperspectral imagery of the Konza Prairie Biological Station in northeastern Kansas was used to evaluate upwelling spectral radiance, prairie spectral reflectance and band ratios of each as potential indicators of vascular plant species richness in a mesic grassland. The extent to which spatial variability in these parameters related to plant species richness also was investigated. A 224 channel hyperspectral data cube acquired in June 2000 by the Airborne Visible and Infrared Imaging Spectrometer (AVIRIS) provided complete coverage of the 400–2500 nm range at approximately 10 nm per channel. After band deletions accounted for detector overlap and strong atmospheric attenuation features, 176 bands were retained for analysis and spanned the 404–2400 nm range. Prairie reflectance was estimated via radiative transfer modeling and scaling to a library spectrum of highway construction material. Data were sampled from pixels having a 19 m ground sample distance (GSD) to represent each of 93 vegetation sampling transects. Reflectance and radiance at mid-infrared wavelengths (e.g., 1553 nm), and band ratios that were based on atmospheric windows in the red, near-infrared and mid-infrared spectra estimated species richness to within 6 to 7 species per transect. The 856 to 780 nm radiance or reflectance ratio yielded maximum adjusted coefficients of determination ($r^2$) of approximately 0.4 in regressions with richness when data from bison-grazed and ungrazed areas were combined. These regressions remained significant ($p < 0.001$) when only ungrazed areas were assessed although $r^2$ reduced to approximately 0.2. Richness was related significantly also to the 433 to 674 nm reflectance ratio for grazed-plus-ungrazed and ungrazed-only areas. In contrast, the effectiveness of the 433 to 674 nm radiance ratio was reduced by atmospheric backscatter. Species richness did not correlate strongly or consistently with transect spatial variability (coefficient of variation or range) in radiance, reflectance or band ratio value, apparently as a consequence of the relatively small area sampled for each transect (approximately 0.5 ha). Relationships between richness and prairie spectral features were explained by the influence of soil exposure on both parameters. Richness and estimated soil exposure tended to increase from ungrazed lowlands, to ungrazed slopes, to ungrazed uplands to grazed areas. Remotely sensed estimates of soil exposure may be particularly useful in addressing plant species richness on grazed grasslands owing to an overall similarity in spectral reflectance among dominant plant species.

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1. Introduction

Biological diversity, the variety in composition, form and function among organisms, populations and communities, is increasingly threatened by human activities (Chapin et al., 2001). The dependence of biodiversity on habitat quality (Pimm et al., 1995) and climate (Francis & Currie, 2003), coupled with current rates of habitat loss and increasingly
strong evidence of anthropogenic climate change (IPCC, 2001), clearly establishes the need for timely assessments of biodiversity at local to global scales. Such assessments are necessary to our understanding of biodiversity and the development of policies and management practices that foster sustainable ecosystems. Remote sensing has begun to contribute substantially to this effort, and increasingly will facilitate the mapping of species and community distributions, evaluations of physical constraints on biodiversity, and biodiversity monitoring and forecasting (Kerr & Ostrovsky, 2003; Stoms & Estes, 1993).

The remote sensing of biodiversity may involve direct detection of organisms or communities or infer their presence based on habitat characteristics and primary productivity (Nagendra, 2001; Turner et al., 2003). Habitat or landscape classifications based on satellite data have been valuable in estimating mammal (Oindo et al., 2003), bird (Jorgensen & Nohr, 1996), butterfly (Kerr et al., 2001) and tick (Cumming, 2000) species diversity. Areas of greatest species richness, the number of species in a particular location, may coincide for plant, bird and insect species (Debinski et al., 1999).

Assessing plant biodiversity by remote sensing relies generally on relationships between species richness and habitat diversity (Gould, 2000; Nagendra & Gadgil, 1999a) and has involved a range in measurement scale (Nagendra & Gadgil, 1999b) and technological approaches. Examples include the use of environmental and topographic data from orbital sensors to estimate plant species diversity in an agricultural landscape (Luoto et al., 2002), and RGB tonal values from aerial photographs to assess grassland species diversity (Waldhardt & Otte, 2003). For arctic tundra (Gould, 2000) and tropical rain forest (Foody & Cutler, 2003) spatial variability in Landsat TM data was linked to patterns of plant species richness.

Extensive remote sensing research in the central US has addressed numerous aspects of tallgrass prairie relevant to patterns and determinants of plant species richness. However, the evaluation of tallgrass prairie biodiversity by remote sensing presents a substantial challenge owing in part to the similarity in spectral reflectance characteristics among the dominant plant species (Walter-Shea et al., 1992). Spectral reflectance measured on the ground easily delineated burned versus unburned prairie (Asrar et al., 1989; Turner et al., 1992). TM data likewise discriminated among these and other grassland management practices (Peterson et al., 2002; Price et al., 2002), and identified cool-versus warm-season cover types (Guo et al., 2000). Ground spectra (Turner et al., 1992) as well as TM data (Guo et al., 2000) indicated responses of near-infrared reflectance to grazing, the primary influence on plant species diversity in tallgrass prairie (Collins et al., 1998; Hickman et al., 2004; Risser, 1988). For shortgrass prairie in northwestern Kansas, plant species diversity as a function of grazing intensity was predicted from TM data (Lauver, 1997). Spatial variability in SPOT or TM data as a measure of landscape texture was sensitive to changes in plant vigor over the growing season and correlated with primary production (Briggs & Nellis, 1991; Knapp et al., 1999). Thus, a landscape texture approach may hold promise for estimating plant species richness given apparent relationships of species diversity with primary production (Knapp et al., 2002; Symstad et al., 2003) and landscape heterogeneity (Moser et al., 2002).

In grasslands, plant species composition and diversity can significantly influence ecosystem productivity (Hooper & Vitousek, 1997; Smith & Knapp, 2003; Tilman et al., 1997) with greatest diversity associated with high spatial heterogeneity of soils or disturbance (Bakker et al., 2003; Collins et al., 1998; Knapp et al., 1999). Tallgrass prairie in particular is characterized by a high plant species diversity compared with other grasslands (Risser, 1988).

In the present study, we utilized AVIRIS imagery of the Konza Prairie Biological Station (KPBS), a tallgrass prairie preserve in northeastern Kansas, to evaluate relationships of plant species richness with upwelling spectral radiance (L), prairie spectral reflectance (R) and band ratios in the 404–2400 nm wavelength range. Denominator band central wavelengths were selected according to their relatively high atmospheric transmittance in the visible, near-infrared or mid-infrared spectral regions. Results for band ratios of L, which was not corrected for atmospheric interference, were compared with results for band ratios of R so that the necessity of correcting for clear-day atmospheric interference in this assessment of plant species diversity could be evaluated. Specific objectives were to: 1) determine the extent to which species richness correlated directly with L, R or band ratio value or their spatial variability; 2) evaluate the importance of an approximate correction for atmospheric interference (scaling to L) in the assessment of diversity, and 3) interpret significant correlations with respect to prairie biophysical characteristics and discuss their potential in remotely sensing plant species diversity on mesic grasslands.

2. Methods

AVIRIS and ground transect data collected in June, 2000, were used to evaluate relationships of plant species richness with spectral features of the Konza Prairie Biological Station (KPBS), a 3487 ha tallgrass preserve and National Science Foundation Long-Term Ecological Research (LTER) site in northeastern Kansas (39° 5’ N, 96° 35’ W). All data were acquired through the KPBS data archives. The KPBS is subject to a mid-continental climate with average monthly temperatures ranging from −2.7 °C in January to 26.6 °C in July. Average annual precipitation is 834 mm with most occurring during the growing season of April through September. Although landscape heterogeneity tends to be relatively low in June (Briggs & Nellis, 1991), earlier studies gave no indication that multi-temporal data would improve the discrimination of tallgrass prairie cover types, which may infer differences in species richness, versus the use of mid-summer data alone (Peterson et al., 2002). Consequently, this
study was based on the single June 2000 acquisition of AVIRIS data.

The KPBS is located in the Flint Hills region, which is characterized by extensive upland and lowland sites and a range in elevation of approximately 80 m. It is divided into 64 experimental watersheds (e.g., Fig. 1) which are subjected to differing fire frequency treatments (1, 2, 4, 10 and 20 yr. burn intervals; Knapp & Seastedt, 1998). Some fire treatments have been in effect since 1972 and others began in 1981. Cattle have been excluded from the KPBS since 1971. In 1987, 30 bison (Bos bison) were reintroduced to 1012 ha which include 10 watersheds subjected to a range in fire frequency (1, 2, 4 and 20 yr. intervals). At the time of this study, bison herd size was approximately 200 individuals.

Vegetation on the KPBS is dominated by the C_4 grasses big bluestem (Andropogon gerardii Vitman), Indian grass (Sorghastrum nutans L. Nash), switchgrass (Panicum virgatum L.), little bluestem (A. scoparius Michaux), rough dropseed (Sporobolus asper Michx.) and sideoats grama (Bouteloua curtipendula Michx.), whereas a variety of C_3 grass, forb and woody species constitute most of the plant species diversity (Freeman, 1998; Smith & Knapp, 2003). Fire, grazing, climatic variability and topography influence patterns of plant species richness separately and interactively. Richness is lowest on annually burned sites and increases with decreasing fire frequency (Collins & Steinauer, 1998; Smith & Knapp, 1999). In contrast, bison grazing increases richness, even when fire is frequent (Collins et al., 1998). Increasing within-season variability in the amount and frequency of precipitation also has been shown to increase plant species diversity (Knapp et al., 2002). Across the topographic gradients at KPBS, species richness is generally greatest on uplands and least on lowlands that are dominated by a few C_4 grasses (Hartnett & Fay, 1998).

Throughout late May and June, plant species richness, defined as number of plant species, was recorded for each of 93 transects established among 12 watersheds within a 14 km² area (Fig. 1). The watersheds have been exposed to a variety of prescribed burning and grazing regimes since 1982 and 1991, respectively. Ten of the watersheds were burned annually in spring (six), fall (two) or winter (two). The remaining two were burned once every four years. Three of the watersheds were grazed by bison and the remaining nine were ungrazed. The watersheds include Florence cherty clay loam soils on uplands, Tully silty clay loam on lowlands, and slopes with rocky outcrops. Only transects dominated by grasses and forbs were included in the study. Transects containing trees and shrubs, which are found primarily in drainages (Fig. 1) were excluded to emphasize the predominant grassland community type of the KPBS. Each transect was comprised of five circular, 10 m² plots arranged along a 50 m transect starting at the 5 m point (Bakker et al., 2003). Richness was derived by compiling data from the five plots and counting the total number of species sampled. A given species was counted only once per transect regardless of its frequency within the transect.

The AVIRIS flyover, conducted by the NASA Jet Propulsion Laboratory, occurred at approximately solar noon on June 22 in a clear sky. Prairie vegetation was green and vigorous, having received 2.6 and 5.8 cm of rainfall on June 13 and 20, respectively. Air temperature ranged from 18.6 °C at pre-dawn to 31.8 °C during mid-afternoon and averaged 24.9 °C. Surface windspeed during 1100–1600 h CDT ranged from 4.5–6.2 m s⁻¹ and averaged 5.5 m s⁻¹. The AVIRIS data cube consisted of radiance calibrated to 12-bit resolution and stored as 16-bit integers in raster format within each of 224 spectral bands that spanned a 374 to 2508 nm range in central wavelength. Full-width-at-half-maximum (FWHM) bandwidths and band increments were approximately 10 nm. The data were georectified to North American Datum 1983, UTM Zone 14N (IMAGINE v. 8.3, ERDAS, Inc., Atlanta, GA) and indicated a 19 m ground sample distance (GSD). Bands 1–3, 30–32, 96, 106–116, 151–169, and 214–224 were deleted owing to strong atmospheric interference or detector overlap. This procedure retained 176 bands in the 404 to 2400 nm range for subsequent processing and analysis. AVIRIS radiance in 16-bit integer format was divided by channel-dependent gain factors to yield upwelling spectral radiance (L) in units of μW cm⁻² nm⁻¹ sr⁻¹. Beyond the band deletions, no further corrections for atmospheric absorption or backscatter were applied to the L spectra.

Additional processing and analysis (SAS v. 6.12, SAS Institute, Cary, NC) was limited to spectra extracted from 7–19 pixels per transect that represented transect location and immediately neighboring terrain (0.25 to 0.7 ha). The total of 1181 spectra for the 93 transects would enable the regression of species richness with mean transect L, an approximation of surface reflectance (R), and band ratio values, and with transect spatial variability (coefficient of
variation or range) in these parameters for each spectral band. The unequal sampling of pixels among transects resulted from the occasional necessity to avoid nearby roads, rocky outcrops or woody vegetation. However, sampling was more uniform among transects than indicated by the range in number of pixels sampled. On the average, 12.7 ± 2.6 (standard deviation) pixels were sampled per transect.

To evaluate potential influences of further corrections for atmospheric interference on regressions of species richness with band ratio values and given that spectroradiometric data for ground reference targets were not available, prairie surface reflectance \( (R) \) was approximated from \( L \), a MODTRAN v. 4.0 radiative transfer simulation, dark-pixel subtraction, and linear scaling to a library reflectance spectrum of highway construction material. MODTRAN simulated the upwelling spectral \( L \) from a rural landscape assuming a 100% surface reflectance throughout the 400–2500 nm wavelength range, a flight altitude of 20 km above the 400 m elevation of the KPBS, a nadir view angle, and a ground-level visibility of 23 km. The high-resolution \( L \) spectrum generated by MODTRAN was resampled (ENVI v. 3.6, Research Systems, Inc., Boulder, CO) to the central wavelengths and FWHM bandwidths of the AVIRIS bands (Fig. 2A). A dark-pixel spectrum was extracted from the KPBS image (minimum pixel value per band, image statistics, ENVI v. 3.6) to estimate backscatter and noise from other sources assuming that actual target \( L \) approached zero. In the violet through green and yellow through mid-infrared spectra, these minimum pixel values represented drainage bottoms and central portions of small ponds, respectively. A first estimate of \( R \) was derived by dividing AVIRIS \( L \) minus dark-pixel \( L \) by MODTRAN \( L \) minus dark-pixel \( L \). This quotient was multiplied by 100 to yield \( R \) in percentage units. This procedure yielded a first-estimate spectral \( R \) of an Interstate Highway 70 (I-70) intersection (Fig. 1, bottom center; Fig. 2B) that was similar to that of asphaltic concrete (Johns Hopkins University spectral library, ENVI v. 3.6).

With respect to sensor view angle along the scan-line dimension, the I-70 intersection was well-placed as a reference target at 7° west of nadir. All transects were located within 1° to 14° west of nadir. Transect-to-reference distance in the scan-line dimension was a maximum of 2.5 km, and 1.8 km or less for all but 7 transects. Thus, to further refine the approximation of spectral \( R \), the ground-level spectral \( R \) of the I-70 intersection was assumed to equal the spectrum of asphaltic concrete. First-estimate \( R \) was multiplied by a linear scaling factor derived for each band so that the resulting final spectral \( R \) of the intersection equaled that of asphaltic concrete resampled (ENVI v. 3.6) to AVIRIS central wavelengths and FWHM bandwidths (Fig. 2B). This scaling procedure was applied uniformly to all transect spectra and thus did not account for spatial variability in atmospheric column water vapor content (Gao et al., 1993; Qu et al., 2003). However, it yielded a mean \( R \) spectrum that was similar to a summer \( R \) spectrum of the KPBS that was derived earlier from a within-pixel atmospheric correction of AVIRIS data (Gao et al., 1993) (Fig. 3). Additionally, the unknown degree of spatial variability in atmospheric water vapor content did not appear to be a significant influence on relationships of species richness with \( R \) (see Results and discussion).

All relationships of species richness with \( L \) or \( R \) were assessed using simple linear regression analysis (SAS v. 6.12). Band ratios were computed by dividing \( L \) or \( R \) in
each band by the same variable in a denominator band that was selected for its relatively high atmospheric transmittance within the visible (674 nm), near-infrared (780, 875, 1042 or 1240 nm) or mid-infrared spectrum (1553, 1623 or 2141 nm) as indicated by the MODTRAN simulation described earlier (Fig. 2C). Species richness was regressed with mean transect $L$, $R$, or band ratio value ($n=7–19$) for each band. Where a relatively strong relationship with species richness was found using data from all 93 transects, the regression procedure was repeated for each of three randomly-selected sub-samples, each comprised of approximately 50% of the data (46 transects). This served to check the consistency with which a particular $L$, $R$, or ratio numerator band yielded a maximal $r^2$ in regression with richness. Relationships of richness with spatial variability in $L$, $R$, or band ratio value were evaluated by regression with transect coefficient of variation (CV) or data range.

To evaluate potential effects of unequal pixel sampling among transects, analytical procedures were repeated using a reduced data set comprised of only 7 pixel spectra sampled randomly for each transect from the full data set. Results based on this uniform sample size were compared with those for the full data set. This comparison was of particular interest in the evaluation of within-transect spatial variability as an indicator of species richness.

### 3. Results and discussion

Plant species richness and AVIRIS spectra for each KPBS transect were sampled at microhabitat ($\leq 0.1$ ha) to within-community ($0.1$ to 1000 ha) scales, respectively, as defined previously (Stoms & Estes, 1993). In contrast with regional to global scale assessments of biodiversity which are based on broad heterogeneity among habitats, species habitat requirements and habitat-type classifications of remotely-sensed data (Nagendra, 2001; Turner et al., 2003), our approach utilized relatively fine spatial and spectral resolutions in comparing species richness directly with radiance ($L$) and reflectance ($R$) spectra within a 14 km$^2$ area characterized by a relatively homogeneous vegetation type. Although the number of species per transect ranged from 16 to 61, the vast majority of transects used in this study were dominated or co-dominated by big bluestem. Species found on the KPBS in addition to big bluestem and the other dominants listed under Methods are documented elsewhere (Freeman, 1998; Towne, 2002). Species observed in the long-term sampling transects are listed at [http://climate.konza.ksu.edu/konza](http://climate.konza.ksu.edu/konza).

Mean $L$ and $R$ spectra based on all pixels sampled ($n=1181$) were similar to AVIRIS spectra reported earlier for the KPBS in summer (Gao et al., 1993) (Fig. 3). The standard deviation of this overall mean was generally greatest in bands
having the greatest $L$ or $R$. The coefficient of variation, or standard deviation as a percentage of the mean, was greatest in the mid-infrared spectrum.

Simple linear regression indicated significant relationships of plant species richness with mean transect $L$ or $R$ throughout the mid-infrared spectrum (Fig. 4). Because the

Table 1

<table>
<thead>
<tr>
<th>Central wavelength (nm)</th>
<th>Adjusted $r^2$</th>
<th>Intercept ($a$)</th>
<th>Slope ($b$)</th>
<th>Standard error of the estimate ($s$)</th>
<th>Adjusted $r^2$</th>
<th>Intercept ($a$)</th>
<th>Slope ($b$)</th>
<th>Standard error of the estimate ($s$)</th>
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<td>0.24</td>
<td>-8.6</td>
<td>33.7</td>
<td>7.2</td>
<td>0.24</td>
<td>1.2</td>
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<td>7.2</td>
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<td>Denominator</td>
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<td></td>
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<td>674 (76)</td>
<td>0.23</td>
<td>80.7</td>
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<td>0.24</td>
<td>-8.6</td>
<td>33.7</td>
<td>7.2</td>
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<td>1.2</td>
<td>2.6</td>
<td>7.2</td>
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<td>-589.3</td>
<td>771.4</td>
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<td>875 (84)</td>
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<td>2.6</td>
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</table>

| Ungrazed only          |               |                |             |                                      |               |                |             |                                      |
| 433 (54)               | 674 (76)      | 0.08           | 61.2        | -11.1                                | 0.25          | 1.2            | 2.6         | 7.2                                  |
| 856 (83)               | 780 (80)      | 0.22           | -543.8      | 714.7                                | 0.20          | 1.2            | 2.6         | 7.2                                  |

Regression analyses were conducted separately for grazed plus ungrazed prairie and for ungrazed-only prairie. Numbers in parentheses are MODTRAN estimates of atmospheric transmittance (percentage) at the central wavelength given the corresponding AVIRIS bandwidth (approximately 10 nm FWHM). For all regressions using the full data set, the probability of a greater value of the $F$ statistic was $p \leq 0.0001$. All regressions remained significant at $p \leq 0.0001$ although $r^2$ values decreased (not shown) when a uniform number of pixels (7) were sampled for all transects. For regressions that were based on data from ungrazed prairie alone, $p \leq 0.001$. 

Fig. 4. Adjusted $r^2$ for simple linear regressions of plant species richness per transect with transect mean $R$ (thick curve) or transect coefficient of variability (thin curve) based on a sampling of 7–19 pixels per transect. Regression analysis was repeated using three random sub-samples, each comprised of approximately 50% of the data (46 transects) (A, B, C) and the full dataset (93 transects) (D). The dotted curves in (D) indicate adjusted $r^2$ for regressions of richness with mean $R$ or transect CV which resulted from a uniform sampling of 7 pixels per transect. Inset numbers indicate central wavelength and $r^2$, respectively, at $r^2$ maxima. Where adjusted $r^2 \geq 0.1$, $p \leq 0.001$ if $n = 93$ and $p \leq 0.018$ if $n = 46$. Where adjusted $r^2 \geq 0.2$, $p \leq 0.0001$ if $n = 93$ and $p \leq 0.001$ if $n = 46$. In a given band, the same conversion of $L$ to $R$ was applied to all image pixels. Thus, adjusted $r^2$ for regressions with $L$ were identical to those shown in A–D.
conversion of \( L \) to \( R \) was applied uniformly among spectra, adjusted \( r^2 \) for regressions with \( L \) were identical to those shown for \( R \). The occurrence of maximal \( r^2 \) in the mid-infrared spectrum was consistent among analyses for three randomly-selected sub-samples each representing 46 transects (\( p \leq 0.018 \) where adjusted \( r^2 \geq 0.1 \)) and the full data set representing all 93 transects (\( p \leq 0.001 \) where adjusted \( r^2 \geq 0.1 \)). For the full data set, richness correlated most strongly and consistently with \( L \) or \( R \) near 1553 nm where the adjusted \( r^2 = 0.24 \) and standard error of the estimate (\( s \)) was 7 species per transect (Figs. 4 and 6; Table 1). At a 1553 nm central wavelength and FWHM of 11 nm (AVIRIS band 127) MODTRAN predicted an atmospheric transmittance of 94% for the conditions described under Methods (Table 1).

If spatial variability in atmospheric column water vapor content had been a significant influence on total spatial variability in \( L \) or \( R \) in accordance with the spectrally-dependent influence of water vapor on atmospheric transmittance, \( r^2 \) for relationships of species richness with \( L \) or \( R \) likewise might have varied with atmospheric transmittance in spectral regions where water vapor is the predominant absorber of solar radiation (e.g., 856–1117 and 1454–1783 nm, Gao et al., 1993). A substantial spatial variability in atmospheric water vapor would tend to increase among-transect variability in \( L \) or \( R \) for strongly-absorbed bands more than for highly-transmitted bands. Consequently, \( r^2 \) would tend to increase with atmospheric transmittance if other sources of variability were not predominant. However, \( r^2 \) for regressions of richness with \( R \), and thus with \( L \) as described previously, within the 856–1117 and 1454–1783 nm spectra as shown in Fig. 4D were essentially constant across the broad ranges in MODTRAN-simulated atmospheric transmittance within these regions (Fig. 5). This was true also for \( r^2 \) within the 1971–2400 nm range, but these were not included in Fig. 5 because atmospheric transmittance in this region is influenced substantially by carbon dioxide and methane as well as water vapor (Gao et al., 1993). Thus, it appears that spatial variability in atmospheric water vapor content was not a significant influence on present results.

Regressions of species richness with band ratios that incorporated denominator bands of relatively high atmospheric transmittance for the visible, near-infrared or mid-infrared spectra yielded \( r^2 \) and \( s \) that were improved only slightly in most cases compared with results for \( L \) or \( R \) at 1553 nm (\( L_{1553} \) or \( R_{1553} \) (Fig. 6; Table 1). However, regressions with \( R_{856}/R_{780} \), \( R_{799}/R_{875} \), or the corresponding \( L \) ratios yielded greater \( r^2 \) of approximately 0.4. Range in ratio value over the full range in richness among all transects (61–16=45 species per transect) was quite small in some cases (e.g., Fig. 6F). This is explained at least partially by the 28–76 nm proximity of numerator and denominator central wavelengths for nearly half of the ratios listed in Table 1. Nevertheless, band central wavelengths that were optimal for the numerator were similar among results for sub-samples and the full data set whether the ratio value range was relatively small or large (e.g., Fig. 7). For this analysis of the full data set, \( r^2 \) and \( s \) for \( L \)-ratio regressions tended to be similar to those from \( R \)-ratio regressions when only near- and mid-infrared bands were used (Fig. 7H; Table 1). However, \( L \)-ratios that incorporated shorter-wavelength bands in the visible spectrum produced different regression results compared with backscatter-corrected \( R \) ratios (Fig. 7G; Table 1). Thus, although the determination of \( R \) was approximate, results emphasize the importance of correction for visible-spectrum backscatter in interpreting spectral indicators of species richness on the KPBS.

In contrast to results based on mean transect \( L \), \( R \) or band ratio value, species richness did not correspond strongly or consistently with spatial CV or data range (Figs. 4 and 6; Table 2). Although regressions involving the CV or range for some band ratios were significant (\( p = 0.05 \), adjusted \( r^2 \) were generally very low at 0.1 or less. However, this approach addressed spatial heterogeneity in prairie spectral features for relatively small areas on the order of 0.5 ha. Apparently, these areas were not sufficiently large to capture a landscape heterogeneity, or texture, that might indicate trends in species richness. Earlier studies on the KPBS addressed larger areas that ranged from approximately 10 ha to several thousand ha and reported a sensitivity of textural indices to seasonal changes in plant vigor and primary productivity (Briggs & Nellis, 1991; Knapp et al., 1999). Given the inverse relationship of aboveground biomass production in prairie vegetation with plant species diversity (Knapp et al., 2002), such measures of landscape heterogeneity might also indicate species richness. In the present case, including the CV or range of a NDVI computed from the AVIRIS data as a surrogate for biomass together with
Fig. 6. Simple linear regressions of plant species richness per transect with transect mean L or R at 1553 nm (A, B), transect mean of the indicated band ratio of L or R (C–F), and the transect coefficient of variation (CV) for the indicated band ratios (G, H). Probabilities of a greater value of the F statistic were $p \leq 0.0001$ for A–F and $p \leq 0.02$ for G and H. Data from bison-grazed and ungrazed prairie are represented by dark circles and open triangles, respectively. These particular regressions are shown because (A) and (B) produced the greatest $r^2$ based on L or R per se, (C–F) can be compared with Fig. 8 and (E) and (F) produced the greatest $r^2$ overall, and (G) and (H) produced the greatest $r^2$ based on within-transect spatial variability.
CV or range of the ratio values described earlier in regressions with richness yielded no significant improvement in $r^2$ (results not shown). This also may have been due to the small areas sampled, but relationships of the NDVI with biomass on the KPBS can be site-specific and differ between years (Weiser et al., 1986) or seasonally (Turner et al., 1992).

Regressions that were significant when the full data set was used tended to remain so when a uniform 7 pixels were sampled for each transect, although $p$ values increased and adjusted $r^2$ decreased (Fig. 4; Tables 1 and 2 legends). Transect means of $L$ and $R$ computed from a greater sampling of pixels apparently were more representative of prairie features that corresponded with richness.

The range in species richness encountered was influenced substantially by including grazed along with ungrazed prairie in the analysis (Fig. 6). Consequently, analytical procedures were repeated separately for grazed versus ungrazed areas. For grazed areas, regressions of richness with mean transect $L$, $R$, or band ratio value, or with transect

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**Fig. 7.** Adjusted $r^2$ for simple linear regressions of plant species richness per transect with transect mean band ratios of $R$. Ratios were computed by dividing $R$ in each band by $R$ at 674 nm (A, C, E, G) or 780 nm (B, D, F, H). Inset numbers indicate numerator band central wavelength and $r^2$, respectively, at $r^2$ maxima. Regressions were repeated using three sub-samples, each comprised of approximately 50% of the data (46 transects) (A – F) and the full dataset (93 transects) (G, H). Where adjusted $r^2 \geq 0.1$, $p \leq 0.001$ if $n = 93$ and $p \leq 0.018$ if $n = 46$. Where adjusted $r^2 \geq 0.2$, $p \leq 0.0001$ if $n = 93$ and $p \leq 0.001$ if $n = 46$. Dotted curves in (G) and (H) indicate results based on $L$ ratios rather than $R$ ratios. These results exemplify the approximate consistency of numerator central wavelength at $r^2$ maximum among regressions that were based on sub-samples and the full data set. Results for denominator wavelengths of 674 and 780 nm are presented to show this consistency for ratios characterized by relatively large versus small numerical ranges in ratio value, respectively (Fig. 6C – F).
CV or range in $L$, $R$, or ratio value, produced adjusted $r^2$ that remained consistently below 0.2 (results not shown). For ungrazed areas, this was true also with the exceptions that $r^2$ were 0.20 or greater for regressions of richness with $R_{433}/R_{674}$, $R_{856}/R_{780}$ and $L_{856}/L_{780}$ (Fig. 8; Table 1). Apparently, interference from atmospheric backscatter resulted in a much lower adjusted $r^2$ for regression with $L_{433}/L_{674}$ (Fig. 8A). Within the ungrazed areas, an influence of topography on richness and ratio value was observed (Fig. 8). Consequently, results for grazed plus ungrazed areas and for ungrazed-only areas may be explained largely by influences of grazing and topography on prairie spectral features.

Bison grazing reduces aboveground biomass of grasses and increases its spatial variability owing to a characteristic patchiness in grazing intensity and consequent patchiness in fuel availability and fire intensity (Knapp et al., 1999). Indeed, lower $R$ in the near-infrared and increased mid-infrared $R$ for grazed versus ungrazed prairie (Fig. 9A) is consistent with an increase in bare soil or senescent vegetation on the KPBS (Asrar et al., 1986). Mean spectral $R$ of ungrazed slopes, ungrazed uplands and all grazed areas

<table>
<thead>
<tr>
<th>Central wavelength (nm)</th>
<th>$L$ ratio variation regression</th>
<th>$R$ ratio variation regression</th>
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<tbody>
<tr>
<td></td>
<td>Adjusted $r^2$</td>
<td>$a$</td>
</tr>
<tr>
<td>Within-transect CV</td>
<td></td>
<td>0.09</td>
</tr>
<tr>
<td>1693 (92)</td>
<td>1623 (94)</td>
<td>0.07</td>
</tr>
<tr>
<td>2091 (89)</td>
<td>2141 (96)</td>
<td>0.05</td>
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</tbody>
</table>

Results were based on data for grazed plus ungrazed prairie. Numbers in parentheses are MODTRAN estimates of atmospheric transmittance (percentage) at the central wavelength given the corresponding AVIRIS bandwidth (approximately 10 nm FWHM). For all regressions, the probability of a greater value of the F statistic was $p \leq 0.02$. All regressions remained significant at $p \leq 0.05$ although $r^2$ values decreased (not shown) when a uniform number of pixels (7) were sampled for all transects.
could be simulated to within 4 percentage units or less by linear spectral mixtures of mean ungrazed lowland and a mean soil spectrum that was computed from laboratory spectra of sieved samples representing KPBS soil types (Fig. 9B). When mean values of $R_{433}/R_{674}$ and $R_{856}/R_{780}$ for ungrazed slopes, ungrazed uplands and all grazed areas were plotted on linear responses of ratio value to soil exposure that were simulated by spectral mixing, soil exposure was estimated to have increased from ungrazed lowlands (unknown but minimum soil exposure) to ungrazed slopes, to ungrazed uplands, to grazed areas (Fig. 10). This indicated that soil exposure was 18–21% greater on ungrazed slopes, 25% greater on ungrazed uplands, and 26–45% greater on grazed areas than on ungrazed lowlands. With respect to grazed areas, this estimate of soil exposure is consistent with the target consumption of aboveground biomass by bison of 25–40% (Knapp et al., 1999). Additionally, when the mixing procedure was applied to simulate responses of the variables

![Fig. 9. Mean spectral reflectance ($R$) of ungrazed lowland prairie (thin solid curve with maximum near-infrared $R$), ungrazed slopes (thick solid curve) and all bison-grazed areas regardless of topography (dotted curve) derived from AVIRIS data, along with a mean $R$ for dried laboratory samples of soil types found commonly on the KPBS (thinnest curve, minimum near-infrared $R$) (A). Differences in $R$ (B) determined by subtracting the mean $R$ of ungrazed slopes, all grazed areas or ungrazed uplands from a linear spectral mixture comprised of 87% ungrazed lowland $R$ plus 13% soil $R$ (thick solid curve), 81% ungrazed lowland $R$ plus 19% soil $R$ (dotted curve) or 73% ungrazed lowland $R$ plus 27% soil $R$ (thin solid curve), respectively. Soil spectra were obtained by the FIFE Information System staff from Stoner et al. (1980) and provided by the Oak Ridge National Laboratory, Distributed Active Archive Center (www.daac.ornl.gov). Owing to short-wavelength noise in the original spectra, mean soil $R$ at wavelengths of 490 nm or less was assumed to be 3%.

![Fig. 10. Simulated relationships of soil exposure with $R_{433}/R_{674}$ and $R_{856}/R_{780}$. These estimated trends (solid lines) were based on linear spectral mixtures of mean $R$ for ungrazed lowland prairie (lowest soil exposure) with a mean soil $R$ derived from data of Stoner et al. (1980) (Fig. 9). Mean values of $R_{433}/R_{674}$ and $R_{856}/R_{780}$ for ungrazed slopes (open squares), ungrazed uplands (closed triangles) and all grazed areas (open triangles) are plotted on the trend lines (compare with Figs. 6C–F and 8).

![Fig. 11. Plant species richness predicted from its relationship with $R_{856}/R_{780}$ for a 14 km$^2$ area on the Konza Prairie Biological Station. The location of this area is shown in Fig. 1. White lines indicate watershed boundaries.](image-url)
in Table 1 to soil exposure, simulated slope inclinations (positive versus negative) were identical to those observed. Consequently, it appears that the observed correlations of plant species richness with prairie spectral characteristics can be explained by degree of soil exposure and the known linkage between richness and disturbance (Knapp et al., 1999). Based on its relationship with $R_{856}/R_{780}$, richness was predicted for the 14 km² area that contained all 93 transects (Fig. 11).

4. Summary and conclusions

Plant species richness on the KPBS could be estimated to precisions of 6 to 7 species within a range of 16 to 61 species per transect by $L$ or $R$ at mid-infrared wavelengths (e.g., 1553 nm) or by band ratios that were based on atmospheric windows in the red, near-infrared and mid-infrared spectra. Adjusted $r^2$ were virtually identical for regressions of richness with $L$ versus $R$ band ratios when highly-transmitted near- or mid-infrared bands were used in the denominator (Table 1). Thus, the additional data processing required to derive $R$ would not have been necessary for identifying the band ratios that best correlated with richness. This suggests that ratios of highly-transmitted $L$ bands might be used in rapid assessments of prairie biodiversity, avoiding the additional expense of processing to $R$.

The ratios $L_{856}/L_{780}$ and $R_{856}/R_{780}$ yielded the greatest adjusted $r^2$ of approximately 0.4 when data from grazed versus ungrazed areas were combined. Regressions of richness with these band ratios remained highly significant ($p \leq 0.001$) although $r^2$ decreased to approximately 0.2 when only ungrazed areas were considered. Richness also regressed significantly with $R_{433}/R_{674}$ for grazed-plus-ungrazed and ungrazed-only areas. By comparison, the correlation of $L_{433}/L_{674}$ with richness was reduced substantially, indicating the necessity of corrections for atmospheric backscatter in the short-wavelength visible spectrum.

Species richness was not related strongly or consistently with transect spatial variability (CV or range) in $L$, $R$, or band ratio value. This contrasts with results of earlier studies that addressed spatial variability in larger geographic areas on the KPBS, but likely was due to the relatively small area sampled for each transect (approximately 0.5 ha).

Relationships of species richness with $L$, $R$, or band ratios were explained by the apparent influence of soil exposure on plant species richness and prairie spectral properties. Richness and estimated degree of soil exposure tended to increase from ungrazed lowlands, to ungrazed slopes, to ungrazed uplands to grazed areas. The use of AVIRIS data and scaling to $R$ proved advantageous in simulating changes in spectral $R$ associated with topography and estimating degree of soil exposure via spectral mixtures of ungrazed lowland $R$ and a library spectrum of soil $R$. Given the consistency with which dry soil reflectance increases with wavelength, this might have been done as well using broader spectral bands. However, the hyperspectral data also enabled regressions of richness with narrow-band ratios that incorporated proximal numerator and denominator central wavelengths and indicated richness most effectively, such as $L_{856}/L_{780}$ and $R_{856}/R_{780}$. Overall, the remote sensing of soil exposure may be particularly useful as an indicator of species richness in grazed grasslands owing to an overall similarity in spectral reflectance among dominant plant species.

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