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The fine-scale mapping of grassland protein densities

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Abstract

A simple and accurate remote sensing technique for the fine-scale mapping of grassland protein densities was developed during a study of sward quality and antelope dispersion in Kenya, East Africa. Using measures of spectral reflectance and a vehicular navigation system, estimates of protein densities were recorded at rates exceeding 1000 samples per hour. Nitrogen analyses confirmed that reflectance measures were accurate predictors of protein density for a variety of grass swards but not for two species of sedge. Because the regression coefficients linking reflectance to protein density differed significantly between sward types, good estimates using this method will require a separate calibration for each type of grassland. By monitoring and correcting for variations in ambient light levels, the method can be used under a wide range of lighting conditions and for long periods. This facilitates sampling sufficiently systematically and intensively that contour plots of protein density can be constructed and then correlated with distributions of underlying abiotic factors, foraging activity of sympatric herbivores, or prior maps to characterize successional and historical change.

Introduction

The fine-scale mapping of plant resources is an important but often challenging aspect of many grassland studies. Detailed maps typically require many accurate measures of plant quality and quantity from a variety of locations. In this regard, classic sampling techniques such as plot clipping or use of a pin-frame are generally too laborious and time-consuming to be of practical use.

Measures of spectral reflectance seem likely to improve this situation. The relationship between green plant biomass and measures of red (R) and near-infrared light (IR) reflectance is now well substantiated for a variety of sown (e.g. Tucker, 1977; 1980; Curran, 1982) and indigenous (e.g. McNaughton, 1976; Pearson *et al.*, 1976; Boutton & Tieszen, 1983; Be'dard & Lapointe, 1987) grass swards. In the field, data of this nature are typically collected using electronic light meters fitted with interference filters (e.g. Miller *et al.*, 1976; Milton, 1980; Mayhew *et al.*, 1984).

Building on this previous work, an automated system for mapping plant protein densities was developed during a study of Thompson gazelle foraging behaviour in the Maasai Mara and Amboseli regions of Kenya. The technique combined a computerized vehicle navigation system with concurrent measures of sward reflectance and ambient light. By calibrating these measures with analyses of grass nitrogen content, plant protein density could be estimated at thousands of locations within a few hours. This paper describes the equipment and methods employed during the study and reports the relationship between spectral reflectance and protein content for six monospecific grass swards, two sites dominated by sedges and four mixed-species swards.

Materials and methods

Spectral analysis

Red light reflectance tends to be inversely correlated with chlorophyll content, while near-infrared light reflectance is positively correlated with overall biomass (Pearson *et al.*, 1976). In the present study, reflectance was measured with two light-sensitive probes (Tektronix portable radiometers; model J6504) mounted side by side onto

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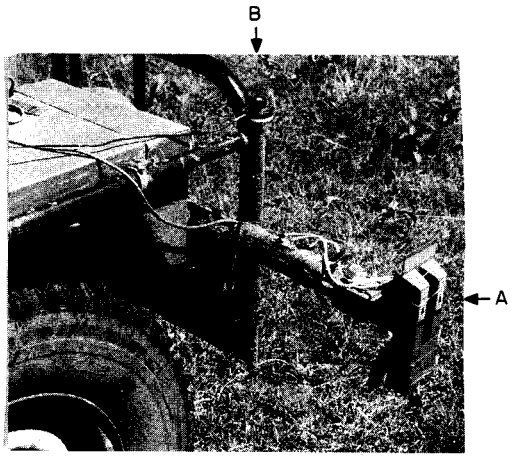

Figure 1. Land Rover with downward-mounted light probes (A) for measuring spectral reflectance. The probe for measuring ambient lighting (B) is mounted upright and adjacent to the other probes.

a small metal plate. Each was fitted with a glass interference filter: one admitting only red light ($\lambda = 650$–670 nm), the other admitting only near-infrared light ($\lambda = 830$–850 nm). This assembly was clamped to the end of a metal bar extending 0·5 m out from the front bumper of a Land Rover, with the filters located 0·5 m above the ground (Figure 1). Ambient light levels were monitored with an upright, unfiltered probe (Licor solar pyranometer; model L1200 SB) (Figure 1). Variations in spectral composition of ambient light were not measured. Leads from the probes were connected to an analogue-to-digital converter (Remote Measurement Systems ADC-1), and the ADC was linked to one of two portable computers (Radio Shack model 100). This Radio Shack allowed the user to specify the frequency at which the ADC and thus the light probes were polled and reflectances recorded. This computer also polled the ADC to obtain ambient light levels using the Licor probe.

Navigation system and mapping

The Land Rover was fitted with a computerized automobile navigation system (manufactured by ETAK, Menlo Park, CA, USA; model 450-C). Relying on wheel-spin ratios and an electronic compass, the system estimated latitude and longitude to the sixth decimal point (approximately 11 cm). This device was connected to the second Radio Shack 100 computer. When used in conjunction with a local map on cassette tape, the ETAK system automatically zeroes out cumulative errors (of the order of 1–2% of the distance travelled since the last correction) by comparing the computed location with the known location of roads. Since no local map tape was available for our sites, cumulative errors were removed by moving to known landmarks (Amboseli) or marker poles placed at 500-m intervals (Maasai Mara) and sending relocation commands to the ETAK with the attached Radio Shack unit. ETAK also kindly supplied us with a control cassette tape which adjusted for the geomagnetic environment experienced by the unit near the equator.

Mapping consisted of driving along a series of overlapping transects (Figure 2). This ensured even and adequate coverage of an area. The two Radio Shacks were programmed in BASIC to collect locational and reflectance data and to synchronize the sampling (programs available from senior author on request). Speeds of driving were 20–25 km h^{-1} while mapping. A programmed pause of 2 s between measurements provided observations approximately every 12 m. This was easily changed by increasing the sampling interval or varying vehicle speed. When linked with the related measures of spectral reflectance, these data allowed fine-scale mapping of resource quality over relatively large areas (Figure 3). In the field, data collected on the Radio Shacks were downloaded at intervals with a portable floppy disk drive, and later transferred to a Macintosh computer and combined into a single file listing the Cartesian coordinates of the vehicle, the spectral reflectances and the ambient light levels at all the sample points.

Sward compositions

A total of 287 grass or sedge samples were utilized for this study. The 91 samples taken on the Koiyaki Group Ranch (approximately 1 km north of the Maasai Mara National Reserve), between June 1989 and August 1990 were either monospecific for, or dominated by, the grass *Themeda triandra*. The remaining 196 samples were collected at Amboseli National Park (September 1988 to March 1989). These consisted of monospecific swards of the grasses *Cynodon plectostachyus* and *C. nlemfuensis*, *Sporobolus kentrophyllus* and *S. spicatus*, and *Psilolemma jaegeri*, or monospecific stands of the sedges *Cyperus laevigatus* and *C. merkerii*, or of mixed

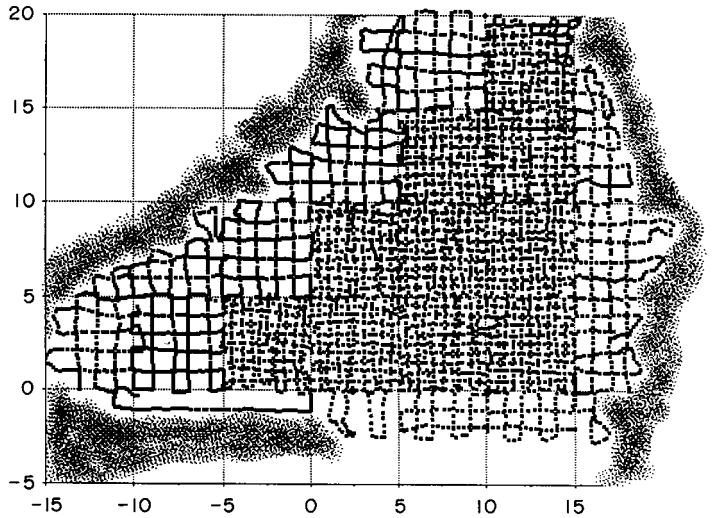

Figure 2. Maasai Mara study area (~ 5 km^2), showing a typical driving pattern while mapping sward quality. This map displays 6051 (x, y) locations where measurements of spectral reflectance were taken over a 2-d period. Stippled areas represent forest.

swards dominated by one of the two *Sporobolus* species or by *Cynodon nlemfuensis*. Sample sizes for each sward type are listed in Table 1.

Calibration methods

To quantify the relationship between spectral reflectances and plant quality, grasses or sedges were first measured *in situ* with the light probes. The sampling area of the probes was circular with a diameter of 58 cm. Once the light measures were complete, ten smaller circles (6 cm diameters) were randomly chosen within the larger sampling circle of the probes. All plant material within each of these smaller circles was cut to ground level and analysed for protein content. All collections were made between 10.00 and 14.00 hours local time from areas that contained at least 10% live plant material. Prior to clipping, three stem heights and five leaf lengths were chosen randomly from within the larger circle and measured. (No leaf lengths were recorded for monotypic swards of the non-leafy sedge *Cyperus laevigatus*.)

Following transport to our field laboratory, plant samples were identified and separated into live (green) and dead (brown) components. Samples were weighed before drying, and then reweighed intermittently until dry weight stabilized. Identifications were made from plant collections and from the literature (Bogdan, 1958; Clayton, 1969; Clayton *et al.*, 1974; Clayton and Renvoize, 1982). Protein contents of both green and dead portions were analysed in the field using a colorimetric method of nitrogen determination (Clifton and Clifton, 1991).

Estimates of 'green protein density' (grams of living plant protein per m^2) were calculated from nitrogen content, sample weight and area sampled. These data were then log transformed and regressed against various algebraic combinations of associated reflectance [all previously shown to correlate with green (live) plant biomass; see Curran, 1980]. Regressions using the 'vegetation index' (IR − R/IR + R) typically yielded the highest correlation coefficients with estimates of green protein density, and this index was used in all subsequent analyses. Data were analysed within a mixed general linear model [Systat MGLH; model: ln(protein density) = ln(veg. index) + species + stem height + leaf length + ln (veg. index) × stem height + ln (veg. index) × leaf length + stem height × leaf length + constant]. Similar

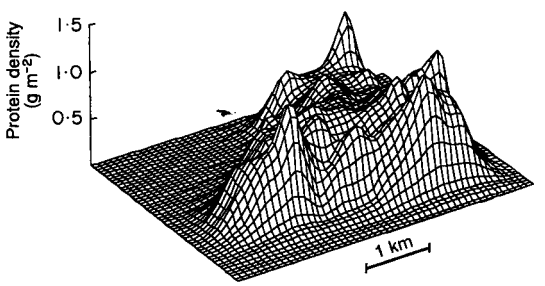

Figure 3. A map of estimated protein density (g m^{-2}) within the Maasai Mara study area. Estimates were generated from a distance weighted least-squares interpolation (d^{-8}).

Table 1. Correlation coefficients for eleven sward types from log-transformed regressions of protein density and spectral reflectance

Sward type	*n*	r^2
Monotypic swards		
Grasses		
Cynodon plectostachyus	9	0·80**
Sporobolus kentrophyllus	8	0·78**
Themeda triandra	37	0·76***
Cynodon nlemfuensis	37	0·74***
Sporobolus spicatus	40	0·70***
Psilolemma jaegeri	14	0·08
Sedges		
Cyperus laevigatus	24	0·08
Cyperus merkerii	9	0·02
Mixed swards dominated by		
Themeda triandra	54	0·80***
Sporobolus kentrophyllus	20	0·79***
Cynodon nlemfuensis	14	0·71**
Sporobolus spicatus	21	0·71***

Samples of *Themeda triandra* came from Maasai Mara; all others were from Amboseli. See text for details (*$P < 0·01$; **$P < 0·001$; ***$P < 0·0001$).

regressions were then undertaken for brown materials.

In addition to the measurements of plant material, 189 separate measures of soil reflectance were also recorded from patches of bare earth (no vegetation present). These soils were subjectively assigned to one of seven discrete colour types (grading from light to dark; see Table 4). The nitrogen content of these soils was not analysed.

Results

Sward-specific green protein density (grams of wet live plant protein per m^2) was highly correlated with spectral reflectance measures for all but one grass and the two sedges (Table 1). These species were deemed inappropriate for reflectance study and removed from subsequent analyses. Stem height and leaf length added no significant predictive value beyond that of vegetation index (Table 2), and were also deleted from further analyses. Regressions using dry weight protein density (grams of dry live plant protein per m^2) generated similar results, though with slightly lower correlation coefficients ($r^2 = 0·56$–$0·79$). Finally, no significant relationship was found between brown protein density (grams of dry dead plant protein per m^2) and spectral reflectance (MGLH; $F_{1,85} = 0·1$; $P = 0·75$). In over 80% of our samples, a minimum of 70% of the total protein density was contributed by the green moiety. This means that, for most of our swards, the inability of the reflectance measures to estimate protein in the dead plant material does not result in major errors in estimates of total protein available.

Spectral reflectance, sward type and their interaction explained 79% of the variance in wet weight protein density, and each of these components made a significant contribution to the variation in protein densities (Table 3). The fact that both the sward type and the interaction term were highly significant implies that there is significant heterogeneity in both slopes and intercepts among the eight graphs shown in Figure 4. It was

Table 2. Mixed linear model analysis of variance in green grass protein density as a function of species, reflectance, stem height, and leaf length

Source	Sum of squares	d.f.	Mean square	*F*-ratio	*P*
Species	6·99	8	0·87	3·28	0·001
ln(veg)	35·85	1	35·85	134·76	0·000
Height	0·01	1	0·01	0·04	0·848
Length	0·03	1	0·03	0·10	0·753
Length × ln(veg)	0·10	1	0·10	0·39	0·534
Height × ln (veg)	0·14	1	0·14	0·53	0·467
Height × length	1·29	1	1·29	4·85	0·029
Error	56·398	212	0·27		

Dependent variable: ln(protein density); $n = 227$; $r^2 = 0·79$.

Table 3. Mixed general linear analysis of variance in green grass protein density as a function of species and spectral reflectance

Source	Sum of squares	d.f.	Mean square	*F*-ratio	*P*
Species	7·00	8	0·88	3·29	0·001
ln(veg)	114·25	1	114·25	430·73	0·000
Species × ln(veg)	7·72	8	0·97	3·64	0·001
Error	58·89	222	0·27		

Dependent variable: ln(protein density); $n = 240$; $r^2 = 0{\cdot}79$.

not important for our purposes to identify which sward pairs contributed most to this heterogeneity. However, the result does imply that separate regressions for different swards will generally be necessary if reflectances are to be used to predict protein densities.

We were concerned whether sites with low cover might show significant differences in vegetation index simply because of differential reflectances from the exposed bare soils. Reflectance measures (given as our standard vegetation index) are summarized for seven categories of bare soil in Table 4. The categories were subjective estimates by us of the darkness of the soil. This table indicates that darker soils tend to produce higher vegetation indices, and that the darkest soil examined had a vegetation index nearly twice that of the lightest soil. However, it is only for the darker soils and the lowest protein densities of plants examined by us that soil reflectances overlapped sufficiently with plant reflectances to alter readings [see Figure 4: the ln(vegetation index) for the darkest soil is about $-2{\cdot}73$ and that of the lightest is $-3{\cdot}35$]. These low protein densities corresponded roughly to about 65% cover for *Sporobolus spicatus*, 70% cover for *Themeda triandra* and 60% cover for the mixed swards dominated by *Sporobolus kentrophyllus*.

We also noted early in the study that variations in the absolute level of ambient light resulted in corresponding changes in measured vegetation index for the same sample. Because ambient light levels change with time of day (see Figure 5 for variation typical in our study sites), or even on shorter scales as cloud cover or dust concentrations vary, we used a sward of median protein density to determine the relationship between measured vegetation index and ambient light levels (Figure 6). The resulting log–log regression was highly significant and linear. Assuming a maximum possible light level of 1130 wm^{-2}, we then used this regression to convert all subsequent vegetation index readings to those expected at a single standard ambient light level. All of the data used in prior analyses were corrected for ambient light levels before analysis.

Discussion

The savannah grasslands of East Africa are a difficult testing ground for any piece of equipment. We were pleasantly surprised by the performance and durability of this mapping system. The navigation equipment weathered deep mud, boulder fields and even the crossing of a flooded river. The light probes withstood severe shaking and bouncing. Despite these hardships, the equipment functioned superbly throughout the study.

Measures of spectral reflectance have historically been used to estimate green biomass, with an inferred link to overall plant quality (e.g. McNaughton, 1976; Boutton and Tieszen, 1983; Mayhew *et al.*, 1984). The strong correlation between reflectance and crude protein density demonstrated here confirms this relationship (also see Everitt *et al.*, 1985). Because crude protein relates directly to levels of digestible crude protein, total digestible nutrients, gross digestible energy and crude fibre (Glover *et al.*, 1957; 1960; Glover and French, 1957; Glover and Duthie, 1958), spectral reflectance becomes a useful predictor of general plant nutritive value. Crude protein levels also typically correlate well with other nutrient densities (e.g. potassium and phosphorus; Boutton *et al.*, 1988)

The relatively high correlation coefficients obtained from nine of the twelve grass swards (from 0·70 to 0·80) are similar to those noted during other field studies (e.g. McNaughton, 1976; Boutton and Tieszen, 1983; Mayhew *et al.*, 1984; Be-'dard and Lapointe, 1987). Mixed-species swards produced results equivalent to those from monospecific swards. Whereas good correlations were obtained between reflectances and both wet and dry samples of green plant material, the technique was not useful for predicting the protein content of brown or dead plant material whether wet or

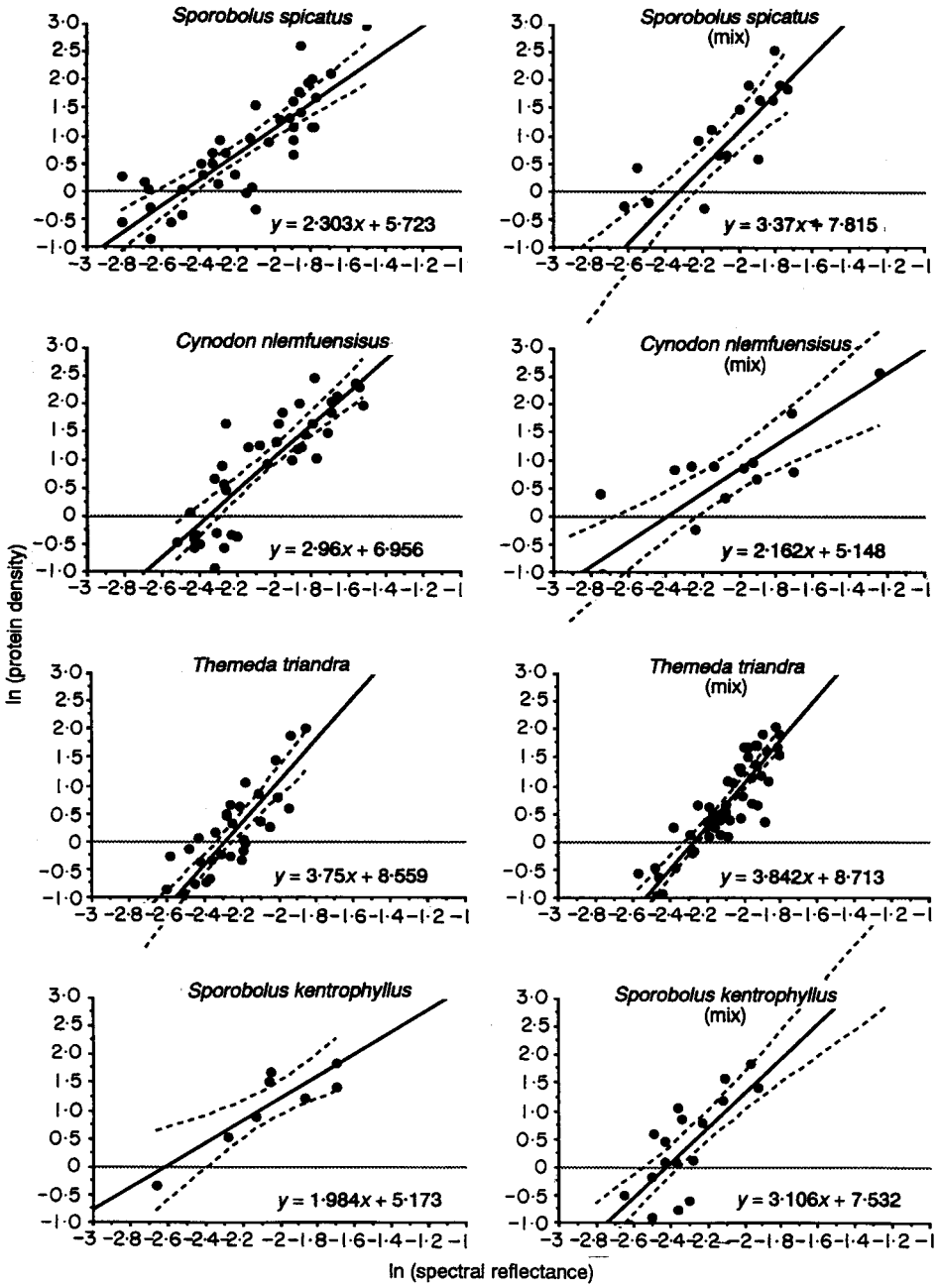

Figure 4. Log-transformed regressions of protein density and spectral reflectance (IR − R/IR + R). Stippled lines represent 95% confidence intervals for the predicted y values. See Table 1 for r^2 and significance levels.

dry. The method thus works well for a variety of swards, but these should be largely green in state. Because our analysis indicates that the slopes and intercepts of this relationship can vary between swards, readings should be calibrated for each new sward type.

In contrast, the spiky-leafed grass, *Psilolemma jaegeri*, and the two sedges, *Cyperus laevigatus* and *Cyperus merkerii*, exhibited extremely poor relationships between sward reflectances and protein densities. These plants are apparently unsuitable for remote sensing techniques. This

Table 4. Mean spectral reflectance (reported as the 'vegetation index': ln(IR − R/IR + R) ± 1 s.e.). All readings taken from bare soil

Soil colour	*n*	Vegetation index + 1 s.e.
White	17	0·035 + 0·002
Light grey	40	0·040 + 0·003
Grey	45	0·046 + 0·001
Dark grey	45	0·054 + 0·003
Light brown	8	0·054 + 0·002
Brown	19	0·061 + 0·003
Dark brown	15	0·065 + 0·003

presumably relates to their physical structure, as all three are essentially non-leafy plants. Boutton and Tieszen (1983) report a similarly poor relationship between biomass and reflectance for small samples of green sedge.

As others have noted (e.g. Colewell, 1974; Curran, 1980; Tucker, 1980), ambient lighting can influence spectral reflectance. As a result, factors such as time of day and cloud cover must be taken into account. In Kenya, light levels were relatively constant only from 11.00 to 14.00 hours, and then only in the absence of clouds or dust. When only a few reflectance samples are needed, it is easy to correct for ambient light variations by using a neutral colour card for reference (Milton, 1980; Mayhew *et al.*, 1984; Be'dard and Lapointe, 1987) or by sampling only at a fixed time of day and if there are no clouds or dust in the air. Clearly, neither of these methods is compatible with the intensity of sampling we are promoting here. The concurrent use of a third light probe to monitor overall ambient light levels appears to be sufficient to bring our correlation values up to the best of those reported by other workers and allowed us to sample in a much broader range of light conditions. We did not monitor changes in the spectral composition of ambient light. Using several additional probes with filters might allow one to monitor any spectral changes induced by clouds or dust and thus reduce the scatter around the regressions in Figure 4 even further.

In our samples, soil colour was likely to influence readings only for the darkest soils and for the lowest protein density swards. Note, however, that most soils darken after rain and, contrary to the conclusions of Mayhew *et al.* (1984), this may be the worst time to make reflectance measurements if plant cover is very low.

Although a variety of stem heights and leaf lengths were encountered during this study, the majority of measurements were taken in relatively short-grass areas where stem heights were well below the light probes. Within the range we encountered, stem height and leaf length added little to the predictive power of the reflectance measures alone. Other studies have also shown that measurements of grass height rarely improve the relationship between plant quality and spectral reflectance (Boutton and Tieszen, 1983).

The system described would work with a variety of vehicles or computers. Tight steering

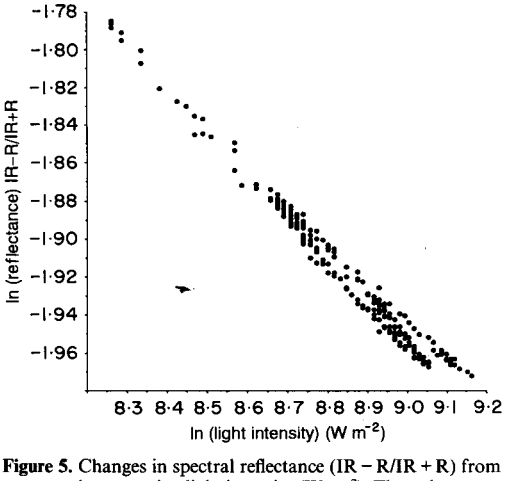

Figure 5. Changes in spectral reflectance (IR − R/IR + R) from one sward at a varying light intensity (W m^{-2}). These data were collected over a 15-min period as cloud shadows passed over the area being monitored. For log transformed variables $r^2 = 0{\cdot}982$.

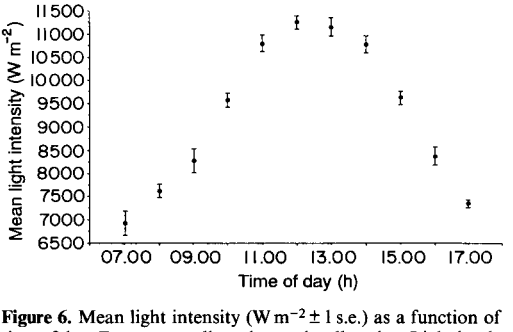

Figure 6. Mean light intensity (W m^{-2} ± 1 s.e.) as a function of time of day. Data were collected on a cloudless day. Light levels from 11.00 to 14.00 hours were not significantly different (Tukey test; $P > 0{\cdot}05$).

linkage and steel belted tyres are the only vehicular requirements. Wheel sensors should be mounted on non-drive wheels and, when possible, the use of four-wheel-drive gearing should be avoided while sampling. Although the Radio Shack computers used in this study were inexpensive, they held relatively few data (32K of RAM) and sampling had to be interrupted at intervals while files were downloaded to a portable floppy drive. Computers with larger storage capabilities would eliminate these breaks in the sampling. Because of incompatibilities between the formats of the software connections of the ETAK and the ADC, we could not use a single Radio Shack to run both digitizing devices. A code-operated switch could have solved this problem, but we were unable to locate one which was battery powered for vehicular use. A battery-powered and code-operated switch would eliminate the need for one of the two computers.

To conclude, this study demonstrates that fine-resolution mapping of protein content for large rangeland areas can be done rapidly and accurately. Data of this nature could enhance a variety of grassland studies. It seems likely that these techniques could also be applied to studies of other plant communities (e.g. low growth shrubs and forbs).

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