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Remote sensing of forage nutrients: Combining ecological and spectral absorption feature data

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ABSTRACT

Forage quality in grassland-savanna ecosystems support high biomass of both wild ungulates and domestic livestock. Forage quality is however variable in both space and time. In this study findings from ecological and laboratory studies, focused on assessing forage quality, are combined to evaluate the feasibility of a remote sensing approach for predicting the spatial and temporal variations in forage quality. Spatially available ecological findings (ancillary data), and physically linked spectral data (absorption data) are evaluated in this study and combined to create models which predict forage quality (nitrogen, phosphorus and fibre concentrations) of grasses collected in the Kruger National Park, South Africa, and analysed in both dry and wet seasons. Models were developed using best subsets regression modelling. Ancillary data alone, could predict forage components, with a higher goodness of fit and predictive capability, than absorption data (Ancillary: $R^2_{adj} = 0.42–0.74$ compared with absorption: $R^2_{adj} = 0.11–0.51$, and lower RMSE values for each nutrient produced by the ancillary models). Plant species and soil classes were found to be ecological variables most frequently included in prediction models of ancillary data. Models in which both ancillary and absorption variables were included, had the highest predictive capabilities ($R^2_{adj} = 0.49–0.74$ and lowest RMSE values) compared to models where data sources were derived from only one of the two groups. This research provides an important step in the process of creating biochemical models for mapping forage nutrients in savanna systems that can be generalised seasonally over large areas.

1. Introduction

Grassland-savanna ecosystems support a high biomass of wild ungulate and domestic livestock populations (Jones and Wilson, 1987). The importance of these systems has led to extensive research on the properties that allow them to support these ungulate populations (du Toit, 2003; Werner, 1991). A component of this research has targeted assessment of food quality; firstly in terms of variations in quality, and secondly in quantifying the quality of the food source.

Within tropical ecosystems, factors that have been linked to differences in forage quality are numerous. Nutrients have been shown to fluctuate between seasons (Grant et al., 2000; McNaughton, 1987; McNaughton, 1990; Prins and Beekman, 1989), between plant species (Jones and Wilson, 1987; McNaughton, 1988; Mutanga et al., 2004b; Seagle and McNaughton, 1992), and between different growth stages of plants (Jones and Wilson, 1987; McNaughton, 1988; Prins and Beekman, 1989). Soil (Allred and Snyder, 2008; Craine et al., 2009; Heitkönig and Owen-Smith, 1998), geology (Grant and Scholes, 2006; Ferwerda et al., 2006), slope and catenal position (Seagle and McNaughton, 1992), and fire (Allred and Snyder, 2008; van de Vijver et al., 1999) are amongst other ecological factors that have been significantly linked to variations in forage nutrient concentrations within savannas.

Given the seasonal and spatial variability in forage quality, and the importance of forage quality for maintaining healthy herbivore populations (Jones and Wilson, 1987; Prins and Beekman, 1989), it is reasonable to assume that livestock or wildlife managers would benefit from a landscape quantification of forage quality. The collection and analysis of forage using wet chemistry techniques, is a time consuming and laborious task, which has been greatly aided

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by the development of rapid analysis techniques using near infrared spectroscopy (NIRS) (Clark, 1989). Using NIRS, absorption features related to physical bond vibrations associated with different nutrients have been identified (Card et al., 1988; Curran, 1989; Fourty et al., 1996). With the advent of imaging spectrometry, in combination with the knowledge derived from the NIRS studies (i.e. known spectral features), it is possible to map the distribution of plant biochemicals at a landscape level (Knox et al., 2011; Mutanga and Skidmore, 2004; Mutanga and Kumar, 2007; Skidmore et al., 2010; Wessman et al., 1988).

In the field of imaging spectrometry for biochemicals, much effort has been placed on predicting the quantity of nitrogen in plants. Besides savanna and grassland systems (Gianelle and Guastella, 2007; Mutanga and Skidmore, 2004; Skidmore et al., 2010), extensive work has been undertaken in forest and cropping systems, where the assessment of plant nitrogen is used as a proxy for net primary production and plant health (Asner and Martin, 2008; Cho and Skidmore, 2006; Goel et al., 2003; Huang et al., 2004; Johnson and Billow, 1996). Evident in these studies is that absorption features (described by the central wavelength) that have been physically linked to foliar nutrient concentrations, were not the only wavelengths or spectral features used as model input variables to predict plant and foliar nutrient content. In many of these studies additional wavelengths and spectral regions were identified to capture the variations in foliar nutrient concentrations (Cho and Skidmore, 2006; Mutanga and Skidmore, 2004; Huang et al., 2004; Johnson and Billow, 1996). All variables should ideally be physically or causally related to the item under study, e.g. for nitrogen, variables might include either known nitrogen absorption features, or wavelengths linked to geological properties or plant age – which have been proven to result in nitrogen variations (Ferwerda et al., 2006; Grant and Scholes, 2006; Owen-Smith, 2008; Skidmore et al., 2010).

Most of the studies quantifying the spatial distribution of biochemicals have been site-specific. By investigators including not only wavelengths that have been physically linked to the foliar nutrient under investigation, they have limited the use of their models to a single moment in time, or a single location. If, however, it is the aim of biochemical remote sensing studies to provide algorithms that can be utilised in multiple sites, and monitor behaviour over time, then variables in a model should be interpretable and transferable between sites and time periods.

The objective of this study was to investigate the potential of combining findings from ecological and NIRS laboratory research to create remote sensing models that can be used to map and monitor forage quality in heterogeneous savanna landscapes. This allows an evaluation as to whether in unison the quality of forage in a savanna can be predicted and monitored in an interpretable and transferable manner from remote sensing data. Combining ancillary and spectral data would provide a sound platform for predicting forage nutrients from remote sensing data and would provide techniques for mapping and monitoring forage nutrients in these systems at a landscape level.

Three sub-goals were defined to provide inputs that allow us to evaluate and discuss the above overall objective. Firstly the ability of environmental factors that have previously been identified as being significantly related to variations in forage nutrient concentrations, and available or potentially available as spatial data, were tested for their ability to estimate forage nutrient concentrations (referred to as *ancillary variables* from here-on). Secondly the potential and predictive ability of spectral features, identified through NIRS that have been physically linked to different nutrients, in predicting forage nutrient concentrations, (referred to as *absorption variables* from here-on) were evaluated. Finally, ancillary and absorption variables were combined to evaluate their combined ability to predict forage nutrient concentrations. We conducted this investigation using spectral, environmental and forage nutrient data collected on grasses, in a wet and dry season, within a sub-tropical savanna system. Our findings are discussed in terms of creating algorithms that can be generalised to temporally map nutrients at multiple sites.

2. Methods

2.1. Study area

The study area was located on the Northern Plains of the Kruger National Park (KNP), South Africa (Fig. 1a), the area is located between 22°49′S, 31°01′E and 22°44′S, 31°22′E, covering an area of approximately 25 × 6 km (Fig. 1b). The location of the study area captures a geological transition, variation in fire treatments, and a herbivore enclosure for rare game species.

The study area is underlain by a geological complex dividing it into granites (west) and basalts (east) (Gertenbach, 1983). The underlying geological complexes have implications for soil nutrient concentrations and consequently on the forage chemistry of the vegetation (Ferwerda et al., 2006; Mutanga et al., 2004a). The vegetation comprises a savanna system with a mixed species grass layer and a tree layer dominated by *Colophospermum mopane*. On the shallow to moderate melanic and vertic clay soils, of the granites, the mopane forms woodlands with an open herbaceous understory. On the moderate deep to deep calcareous duplex clay soils, of the olivine rich basalts, the mopane forms an open shrubland, with a dense herbaceous understory (Venter, 1990).

The herbivore enclosure (“N’washitsumbe” or “Roan Enclosure”[2]), was created in 1967 to act as a breeding area for roan antelope (*Hippotragus equinus*). The exclusion of large browsing herbivores over this extended period, has resulted in an altered woody vegetation structure when compared with the surroundings (Asner et al., 2009; Levick and Rogers, 2008). The enclosure has a greater woody structural diversity in terms of tree species and size variation of the trees. Differential fire management inside and outside the enclosure has further contributed to the aforementioned structural variation (Ferwerda et al., 2006; Levick et al., 2009).

2.2. Data collection

2.2.1. Field sampling

Field sampling (collection of spectra and grass samples) was carried out twice in 2007. Sampling was first conducted in the late wet (late growing) season (mid March to beginning April), and again in the early dry season (May) to capture grass senescence. In the wet season 43 sites were sampled, these sites were again resampled in the dry season thereby creating a paired seasonal dataset. Due to improved weather conditions for spectral measurements, an additional 19 sites were sampled in the dry season (totalling 62 sites for the dry season) (Fig. 1b).

The location of the field sites were defined in an earlier study by Mutanga et al. (2004a). Mutanga et al. (2004a) selected 96 sites using a stratified clustered-random sampling. The area was stratified into open grasslands, mixed woodland and woodland based upon a land cover classification map obtained from the scientific services division of the KNP. Using S-PLUS, *x*–*y* coordinates were randomly generated, plots were then located in the field using GPS (Garmin 12XL, with an estimated 3 m accuracy). Purposive sampling included five samples on known natural salt licks. Sixty-two of these sites were sampled in this study. During an earlier study it was determined that for these sample sites there

[2] www.sanparks.org/parks/kruger/conservation/scientific/exclosures.

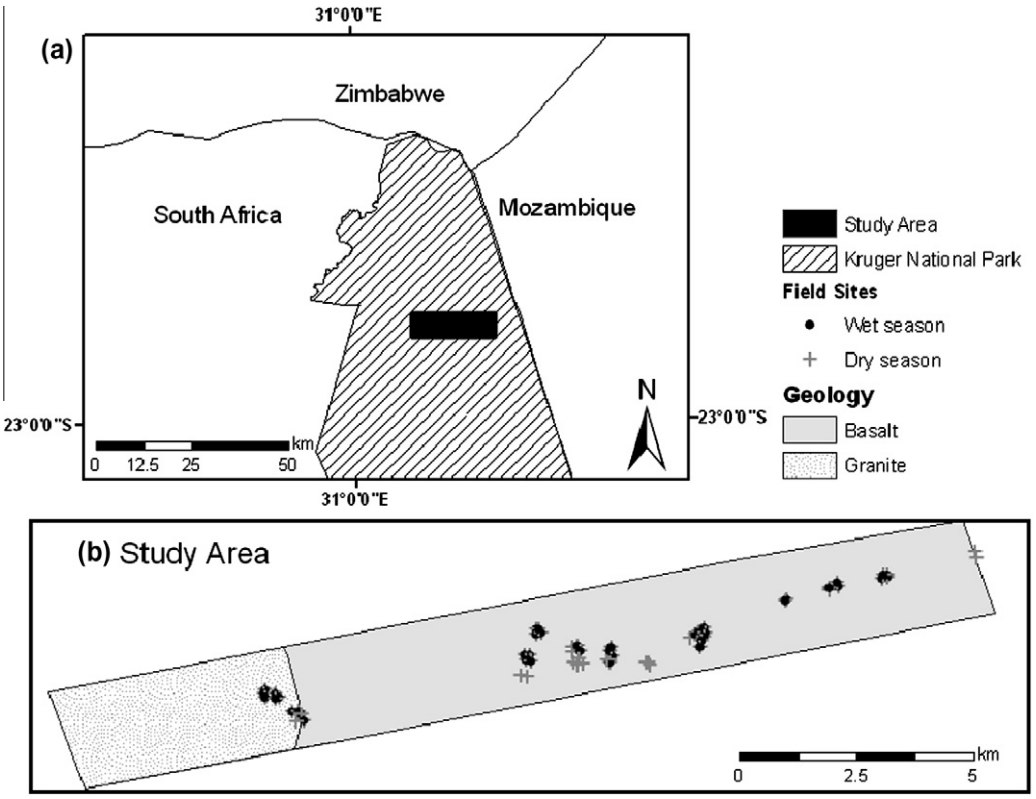

Fig. 1. (a) Location of study area within the Kruger National Park (KNP), South Africa. (b) distribution of the field plots, within the study area, measured in the dry and wet season. The study area delineated in (a) is the border of sub-figure (b) with the field plots distributed diagonally across this study area.

was no obvious spatial dependence, or spatial clustering of the samples (Skidmore et al., 2010).

A plot of 15×15 m was laid out at each site. Within each plot, cover of trees, grasses and bareground were independently visually estimated by two researchers. The results were then compared to ensure that they did not differ by more than 5% from one another. Through this method it was confirmed that for cover estimations between 25–80% cover both researchers agreed on more than 95% of their estimates. In this way the researchers felt confident that they could identify the species covering greater than 30% of the plot, and thus the dominant species could be recorded. The dominant grass and tree species were recorded. Using a hand-held ASD Fieldspec Pro FR spectrometer (Analytical Spectral Devices, Inc.) spectra were taken of the dominant grass species and any other grass species that was estimated to cover an area greater than 30%. The ASD Fieldspec Pro FR spectrometer has a 512 element Si photodiode array that covers the 350–1000 nm range, with a spectral resolution of 3 nm, and a sampling interval of 1.4 nm, and two separate, TE cooled, graded index InGaAs photodiodes that cover the 1000–2500 nm spectral range, with spectral resolutions of 10 nm and sampling intervals of 2 nm. On collection of a spectrum the instrument internally resamples the spectrum to produce a continuous spectrum with 1 nm resolution. These resampled spectra were used in this study. The spectral sampling was performed from a height of approx. 1 m above the grass canopy with an 8° fore-optic creating an IFOV with a diameter of approx. 14 cm. Five spectra were taken per plant canopy, and a minimum of five separate plants of a species were measured in each plot, therefore a minimum of 25 spectra per dominant species per plot were recorded. During spectral measurement it was ensured that bare ground was minimised. Prior to spectral measurement of each plant, a spectrum was taken of a calibrated spectralon panel (Labsphere, Inc, Sutton, NH), this allowed radiance measurements to be converted to reflectance values. Spectra collected per measured species in each plot were averaged to create a single species per plot sample spectrum.

Following spectral measurements, grass samples, of each measured species, were collected. For each species five whole grass plants were clipped at approximately 2 cm above ground level. Per species the clipped samples were pooled, bagged, and dried at 70 °C for 48 h. Following drying, samples were ground through a 1 mm steel mill and transported to The Netherlands for chemical analysis.

2.2.2. Spectra evaluation

Prior to model building all sample spectra were visually-assessed for noise. Particular attention was paid to noise within the blue and short wave infrared spectral regions (SWIR), being regions strongly affected by atmospheric conditions including cloud cover. From all spectra the following spectral regions were consistently noisy and were therefore removed from the analysis, these include wavelengths between 989–1010 nm which are linked to the detector overlap of the spectrometer, regions 1375–1475 nm and 1775–1990 nm associated with strong water absorption features, and wavelengths above 2340 nm associated with the increased SNR as the edge of the detector range. In addition to these spectral regions six spectra, three taken in the wet season and three in the dry season were found to be noisy (i.e. have high variation) across the entire spectrum. The field notes were compared against these identified spectra and it was verified that during collection of these samples there had been cloud presence therefore increasing the likelihood of spectral noise. These six samples were therefore excluded from further analysis. In total, therefore, 40 samples were included in the wet season analysis, and 59 samples for the dry season.

Table 1
Description of the ancillary variables used in this study.

Variables	Type	Description
Slope	Continuous	Expressed in degrees
Altitude	Continuous	Expressed in metres above sea level (m asl)
Aspect	Categorical	Initially calculated in degrees, and then converted into four cardinal points N(315°–45°), E(45°–135°), S(135°–225°) and W(225°–315°)
Geology	Categorical	Broad geological division of basalt or granite
Geo_{Ven}	Categorical	Geological classes based on work of Venter (1990). Within the study area four geological classes were defined
Sl_{Knp}	Categorical	Soils map based on the South African soils classification system (Macvicar et al., 1977). Within the site seven soil layers were identified
Sl_{Ven}	Categorical	Soils map based on the work of Venter (1990). Within the site, three soil layers were identified
Fire	Categorical	Frequency of fires over a five year period prior to sampling. Three classes were defined in terms of fire frequency: none, once and twice
Species	Categorical	Plant species sampled in the field. Eight separate species were identified, plus a mixed species class, yielding nine separate categories
Plant age	Continuous	Plant age variation using a continuous scale was generated using the spectral data collected in the field, and applying the PhIX algorithm (Knox, 2010)
REP*	Continuous	Two methods for calculating the red-edge were applied, REP_d was derived by determining the wavelength location of the maximum first derivative, between the Red and NIR spectral regions, and REP_c was calculated using the linear extrapolation method of Cho and Skidmore (2006)

REP* = Red Edge Position.

2.2.3. Nutrient analysis

The dried and ground samples were analysed for their chemical constituents, in the laboratory of the Resource Ecology Group, Wageningen University, The Netherlands. The three forage components that we considered in this study are nitrogen and phosphorus and fibre content. Nitrogen and phosphorus were analysed using a modified Kjeldahl procedure, samples were initially digested in a mixture of sulphuric acid, selenium and salicylic acid (Novozamsky et al., 1983). Digestion was then followed by colorimetric measurement using a continuous flow analyser (SKALAR SAN plus). Fibre content (Acid Detergent Fibre – ADF) was determined according to the ANKOM filter bag procedure, using an $ANKOM^{200/220}$ fibre analyser (ANKOM Technology, Macedon, NY, USA). All concentrations are expressed as percentage nutrient, on a dry matter basis (% DM).

2.2.4. Ancillary variables

Ancillary variables that were either available or potentially producible in vector or raster format or could be generated from remote sensing data, and had been linked to variations in forage nutrient concentrations, were compiled for each sample site. Geology, soil and fire data were obtained from the GIS and Remote Sensing Centre,[3] Scientific Services, Kruger National Park. Slope, aspect and altitude data were generated from a resampled Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) – digital elevation model, obtained for the site, in June 2006. The DEM product has a spatial resolution of 30 m and is recorded to have an absolute vertical and horizontal accuracy of 10 m. Plant age and the Red Edge Position were generated from the spectra taken in the field. The red edge position is identified as an ancillary variable as this variable although influenced by the width of the red absorption feature, has been shown to correlate with both leaf area index (LAI) and biomass estimation (Cho and Skidmore, 2006; Darvishzadeh et al., 2008a). Both LAI and biomass are environmental variables considered important in the description of vegetation condition and structure. Although no grass species map currently exists for this area, studies have shown that imaging spectroscopy potentially provides a means to create such maps (Irisarri et al., 2009; Schmidt and Skidmore, 2003). Species data collected in the field was therefore included in the analysis, based on the premise that given the appropriate collection of data and analysis such a map could be generated from spectroscopic data. A description of all the ancillary variable layers that were used in this analysis are presented in Table 1.

[3] www.sanparks.org/parks/kruger/conservation/scientific/gis/.

2.2.5. Absorption variables

Only wavelengths that have been physically linked to each of the forage nutrients were selected for this analysis. These physically linked wavelengths have been determined through near infrared spectroscopic (NIRS) studies (detailed in Table 2). The features are associated with the excitation and reaction of molecular bonds at specific wavelengths.

Nitrogen, phosphorus and fibre concentrations are not directly measured, but rather their association with plant compounds are used to derive their concentrations. Total nitrogen measured is associated with molecular bonds of protein, chlorophyll and nitrogen molecules found within the plant (Curran, 1989).

Within plants, phosphorus concentration is much lower than the concentrations of either nitrogen, or fibre. The low phosphorus concentrations reduce the ability to directly detect this nutrient through spectral signatures (Kokaly et al., 2009), therefore an associated link is made with respect to the functioning of phosphorus in a plant's development. Within plants, phosphorus is primarily associated with plant metabolic processes (Schachtman et al., 1998). We therefore spectrally associated phosphorus concentrations to sugars and starches, as representative end products of metabolism.

Fibre is located within plant cell walls, and is a combination of hemicellulose, cellulose and lignin compounds. In NIRS studies for determining forage quality, cellulose and lignin have been extensively studied and their absorption features identified (Curran, 1989; Fourty et al., 1996; Himmelsbach, 2000). The spectral features associated with both of these compounds are used to predict the concentration of fibre within the samples. The spectral absorption features, used as input for the modelling for each of the forage nutrients, are listed in Table 2.

For each of these forage components some of the identified absorption features coincided with noise regions identified in the spectral evaluation (identified with a ^{d} in Table 2), these have therefore been omitted from the remainder of the analysis.

2.3. Model development

One of the assumptions of applying linear regression modelling is that variables are not collinear (Crawley, 2006). The selected wavelengths for each of the nutrients (in both seasons) were found to be highly correlated. By applying a principal component analysis to these absorption feature wavelengths the collinearity between bands was reduced. These principal components (PC) were then used as input variables for the models. Within the ancillary variables, collinearity was found between variables that measured the same environmental parameters, e.g. the geological classes, soil

Table 2
The wavelength absorption features selected for predictive analysis of the forage nutrient concentrations. These wavelength centres have been physically linked (through bond vibrations, excitations) to each of the forage nutrients.

Nutrient	Absorption feature wavelength centres (nm)
Nitrogen[a]	430, 460, 640, 660, 910, 1020, 1510, 1690, 1730, 1940,[d] 1950,[d] 1980,[d] 2060, 2130, 2180, 2240, 2300, 2350[d]
Phosphorus[b]	970, 990,[d] 1450,[d] 1490, 1530, 1540, 1580, 1780,[d] 1900,[d] 1940,[d] 1950,[d] 1960,[d] 2000, 2080, 2100, 2250, 2270, 2280, 2320
Fibre[c]	1120, 1200, 1420,[d] 1450,[d] 1490, 1540, 1690, 1730, 1736, 1780,[d] 1820,[d] 1924,[d] 1940,[d] 1950,[d] 2100, 2232, 2262, 2270, 2280, 2310, 2320, 2340,[d] 2350,[d] 2380[d]

[a] Features associated with protein, chlorophyll and nitrogen (Curran, 1989; Fourty et al., 1996).
[b] Features associated with starch and sugar (Curran, 1989; Fourty et al., 1996).
[c] Features associated with cellulose and lignin (Curran, 1989; Fourty et al., 1996; Himmelsbach, 2000).
[d] Features not analysed because they coincide with regions removed because of high signal noise (see Section 2.2.2).

classes and the two REP calculations. All variables were included as input into the modelling process, but selected output models were checked to ensure they did not include collinear ancillary variables (Crawley, 2006). Prior to the modelling each variable was correlated against the respective nutrients to determine how each individually explained the nutrient concentrations. For the continuous variables a Pearson's correlation was calculated and the r values are presented. For categorical variables a linear model was created between the variable and nutrient and the Adjusted R^2 $\left(R^2_{adj}\right)$ values are presented. The results from these analyses are presented in the Supplementary tables S1–S3.

Although stepwise regression is effective for developing multivariate models, it has been shown to be affected by the order in which variables are entered into the modelling procedure (Crawley, 2006; Grossman et al., 1996). An exhaustive best subsets regression method, is an effective means to minimise this limitation of the stepwise regression procedure. This regression approach can also be set to limit the number of variables contained within a model, thereby avoiding the problem of over-fitted models (Furnival and Wilson, 1974).

"Best subsets regression" (Implemented in R (R Development Core Team, 2008), using the "leaps" (absorption) or "bestglm" (ancillary) packages (Furnival and Wilson, 1974)) was implemented, for each forage component, in each season, based firstly on ancillary variables, and then on absorption variables (as the converted PCs). The "best subsets regression", compared and selected models based on the lowest Akaikes Information Criteria (AIC) value (Crawley, 2006). The generalised linear modelling (GLM) applied in the "bestglm" package to the ancillary data, transforms each of the ancillary variables into a dummy variable prior to modelling. Because the ancillary input variables contained collinear features, it was verified that the variables selected in the top model, by the "best subset regression" method, were free from collinearity. If collinear variables were found, the next best model was evaluated, until a model free from collinearity was found.

For each forage component, in each season, the ancillary and absorption (PC) variables selected in the analysis above, were combined into an ancillary + absorption model. Stepwise regression (including backward and forward selection), was then applied to these combined models, to create a significant parsimonious model that predicted forage component concentrations in a particular season. It was verified that the variables included in these final models were free from collinearity.

On all the final models selected in the analysis, the selected models where then run through a leave one cross validation (LOOCV) procedure. For each iteration in the LOOCV procedure the Adjusted R^2 $\left(R^2_{adj}\right)$ and root mean square error (RMSE) values were recorded. These R^2_{adj} and RMSE values were then averaged and the final values presented are the mean Adjusted R^2 and RMSE value. For validation the R^2 and RMSE value were calculated by relating the predicted value generated during the LOOCV procedure to the observed value.

Using AIC, for each forage nutrient, in each season the three selected models were then compared (i.e. the ancillary, absorption and combined models). The models with the lowest AIC values were considered to be the best models for predicting forage nutrient concentrations. The results of this analysis allow us to provide suggestions as to model variables suited to analyse forage nutrients in a heterogeneous savanna ecosystem, using remote sensing data.

3. Results

In agreement with earlier studies (Grant and Scholes, 2006; McNaughton, 1990) we found that the forage component concentrations differed significantly between the dry and wet seasons (Table 3). The values for the different forage nutrients are comparable with those observed for this region (Grant and Scholes, 2006; Treydte et al., 2008).

3.1. Ancillary variables

Models built using ancillary variables alone (i.e. environmental links to nutrients), showed that between 42–74% of the variation in forage nutrients could be explained. The selected models derived from the "best subsets regression" are presented in Table 4 (the respective model coefficients are presented in the Supplementary tables S1–S3). All variables, included in these models, were significant contributors to explaining the respective forage nutrient concentrations.

Species explained the concentration of forage components, irrespective of the season. Soil type variables were also significant in their contribution to explaining differences in forage concentrations, being a variable type selected in four out of the six models. The finer detail provided by the South African soil classification system (Macvicar et al., 1977), compared to the classification system of Venter (1990), enhanced the ability of most models to estimate the forage contents. The REP is only selected to estimate nitrogen concentrations, supporting the earlier findings of Cho and Skidmore (2006) and Mutanga and Skidmore (2007). Plant age significantly contributed to explaining nitrogen, and fibre in the wet season (Table 4).

Within the KNP the geological stratification into the basaltic east and granitic west has been used to describe broad variations observed in nutrients (Grant et al., 2000; Grant and Scholes, 2006; Skidmore et al., 2010). Our findings show that when trying to estimate the concentrations of nutrients that geological strata, in combination with soil strata, significantly contributed to explaining foliar phosphorus levels in the dry season.

3.1.1. Absorption variables

The model variables, and predictive ability of models, developed with only spectral data (converted to PC data), associated with

Table 3
Results from the chemical analysis of the field samples.[a] In the final column results of *t*-tests[b] comparing the mean forage nutrient levels in the wet (40 samples) and dry (59 samples) seasons are shown.

Nutrient	Season	Range (% DM)	Mean (% DM)	*t*-test
Nitrogen	Wet	0.6–2.2	1.1 ± 0.37	
	Dry	0.4–1.5	0.7 ± 0.20	$t = 7.02$,*** $df = 62.25$
Phosphorus	Wet	0.1–0.5	0.2 ± 0.09	
	Dry	0.1–0.4	0.2 ± 0.09	$t = 2.84$,*** $df = 89.33$
Fibre	Wet	34.1–49.7	41.4 ± 3.53	
	Dry	35.8–51.1	43.4 ± 3.18	$t = -2.89$,*** $df = 77.51$

± the standard deviation of the mean.
[a] As a result of rounding some values appear similar.
[b] *t*-tests (using a Welch modification for unequal variances) were calculated after the data were arc-sine transformed.
*** Significance level of *t*-tests, 0.01.

Table 4
The significant model variables for ancillary variables, for each forage nutrient in the dry and wet season. The model selection was made by applying a "best subsets regression,[a]" with all the variables included in Table 1. All variables had a significant (*p*)-value less than 0.05, the model coefficients are presented in the Supplementary data S1–S3.

Nutrient	Season	cal[b] R^2_{adj}	cal RMSE (% DM)	LOOCV[b] R^2_{adj}	LOOCV RMSE (% DM)	Model variables
Nitrogen	Wet	0.74	0.19	0.55	0.15	Aspect, Fire, Plant Age, REP_c, Species
	Dry	0.67	0.12	0.31	0.17	Plant Age, REP_d, SI_{Ven}, Species
Phosphorus	Wet	0.42	0.07	0.12	0.09	SI_{Knp}, Species
	Dry	0.64	0.05	0.52	0.06	Geo_{Ven}, SI_{Knp}, Species
Fibre	Wet	0.70	1.94	0.49	2.41	Plant Age, SI_{Knp}, Species
	Dry	0.50	2.24	0.44	2.34	Species

[a] Best subsets regression" implemented in R (R Development Core Team, 2008), using the "bestglm" library.
[b] cal = average of the R^2_{adj} and RMSE calculated while implementing a leave one out cross validation (LOOCV).

Table 5
The significant principal components (PC) selected using "best subset regressions[a]" for each forage nutrient, in each season. The values in parenthesis are the wavelengths (nm) with the highest eigen loading values (greater than ±0.5) associated with that PC. The model coefficients for these selected models are presented in the Supplementary data S1–S3.

Nutrient	Season	cal[c] R^2_{adj}	cal RMSE (% DM)	LOOCV[c] R^2_{adj}	LOOCV RMSE (% DM)	Model variables
Nitrogen	Wet	0.45	0.27	0.38	0.29	PC2(910, 1020), PC4(640, even[b]), PC11(2180)
	Dry	0.42	0.16	0.23	0.18	PC2(910, 1020), PC4(even), PC5(430, 460), PC9(2240), PC10(2060), PC11(2130)
Phosphorus	Wet	0.34	0.08	0.23	0.08	PC2(970), PC5(1490, 2000), PC7(2320, even), PC8(2270)
	Dry	0.24	0.08	0.17	0.08	PC2(970), PC7(2100), PC10(1530, even- 1490, 1540, 1580)
Fibre	Wet	0.11	3.33	0.02	3.49	PC9(2262), PC14(1730,1736)
	Dry	0.51	2.22	0.44	2.38	PC3(even), PC6(2232), PC8(2310), PC9(2310), PC10(2100)

[a] Best subsets regression implemented in R (R Development Core Team, 2008), using the "leaps" library.
[b] "even" the remaining wavelengths either listed or indicated, for a particular forage nurient (Table 2). The "even" wavelengths had loading weights less that ±0.5 but were similar in value.
[c] cal = average of the R^2_{adj} and RMSE calculated while implementing a leave one out cross validation (LOOCV).

physical bond vibrations, are presented in Table 5 (the respective model coefficients are presented in the Supplementary tables S1–S3).

Absorption feature variables could better predict (higher R^2_{adj} and lower RMSE values) the concentration of a forage component, when the concentration levels were highest in the plant (e.g. nitrogen/phosphorus in the wet season) (Table 3 vs. Table 5). Thirty four percent of the variation in foliar phosphorus concentrations, was explained by using absorption features, associated with sugars and starch.

3.1.2. Combined data

A combination of absorption data and ancillary data did not always lead to forage nutrient models with higher prediction accuracies (Table 6 vs. Tables 4 and 5). By combining both data sources and applying the stepwise regression procedure resulted in only half of the tested models being more parsimonious and having lower RMSE values. For the remaining models the ancillary variable models proved to be the most parsimonious model. The respective model coefficients derived from these models are presented in the Supplementary tables S1–S3. Similar to the result where only ancillary variables were used for modelling, we found that when combining ancillary and absorption variables, the species variable was again a significant contributor in all the selected forage component models. Soil type data also significantly contributed to four out of the six forage models.

3.1.3. Model comparisons

The concentrations of any of the forage components studied here, in either the wet or dry season, could be predicted with a higher degree of precision, using the ancillary data alone compared to using only the absorption datasets (Table 4 vs. Table 5).

A statistical comparison of the models (using AIC), showed that the six models selected in the combined data approach were the most suitable models (in terms of parsimony and predictive ability) for estimating forage nutrient concentrations (Table 6). Only

Table 6
Combined (ancillary+absorption) model variables. Model variables were selected through a stepwise selection procedure. The input variables were a combination of the variables included in the best models from the ancillary (Table 4) and absorption spectral data (Table 5). The model coefficients for these selected models are presented in the Supplementary data S1–S3.

Nutrient	Season	cal[a] R^2_{adj}	cal RMSE (% DM)	LOOCV[a] R^2_{adj}	LOOCV RMSE (% DM)	Model variables
Nitrogen	Wet	0.74	0.19	0.55	0.15	Aspect, Fire, Plant Age, REP_c, Species
	Dry	0.70	0.11	0.37	0.18	PC2, PC10, REP_d, Sl_{ven}, Species
Phosphorus	Wet	0.49	0.07	0.12	0.1	PC8, Sl_{knp}, Species
	Dry	0.64	0.05	0.52	0.06	Geo_{ven}, Sl_{knp}, Species
Fibre	Wet	0.70	1.94	0.49	2.41	Plant Age, Sl_{knp}, Species
	Dry	0.64	1.92	0.36	2.14	PC3, PC8, Species

[a] cal = average of the R^2_{adj} and RMSE calculated while implementing a leave one out cross validation (LOOCV).

three of these models contained data from both ancillary and absorption spectral sources, the remaining three models were identical to the ancillary data models.

Validation of the predictive models showed that in particular Phosphorus during the wet season is poorly predicted. In general the validation results were highest in the combined models, except for the dry season fibre which had higher predictive capabilities with the ancillary data and spectral data alone.

4. Discussion

In this study we show that using remote sensing and imaging spectrometry it is possible to map forage biochemicals in a repeatable and ecologically sensible way. We have identified for three forage components (nitrogen, phosphorus and fibre) remote sensing derived variables – based on ecological and spectroscopic theory, that predict each of the respective forage components in both the dry and wet season. These variables, could be used as a base from which to generate algorithms, for estimating forage quality in savanna regions.

This study has shown that irrespective of the forage components being considered, temporally universal prediction models cannot be created. Although there are variables that significantly contribute to forage component models irrespective of season (e.g. species and soil type data for foliar phosphorus), additional variables are required in different seasons.

For all forage components, species were found to contribute significantly to prediction models. For multiple plant nutrients, it has been shown that different species display variations in the means they store, or translocate nutrients through the plant (Chapin, 1980). These interspecific differences would be the likely reason that the species variable is found to be significant in explaining nutrient variations in different seasons.

In this study, species information was not derived from remote sensing data. Species were clearly demonstrated to be the single most important variable in modelling savanna forage components (Table S1-S3), this outcome highlights the need for research to be pursued in species mapping with remote sensing. In generating this variable from imaging spectrometry data, it is likely that information will be required from numerous regions of the spectrum (Schmidt and Skidmore, 2001; Schmidt and Skidmore, 2003). Studies where species have been spectrally separated, have highlighted that spectral features selected have been related to physico-chemical regions (Vaiphasa et al., 2007), and that vegetation structure strongly influenced the separability of species (RibeirodaLuz and Crowley, 2010). In using species information for mapping of nutrients, in combination with absorption features, the relationship between variables associated with nutrients and plant physical status should be investigated.

During the wet season water absorption features dominate vegetation spectra. These effects are particularly prominent in the SWIR region (1400–3000 nm) of the spectrum (Elvidge, 1990; Kokaly and Clark, 1999), and the cellulose and lignin features are masked by water features. For nitrogen and particularly fibre we see this influence in the outcomes of the components selected. During the wet season few PC with high loadings of wavelengths within the SWIR2 (2000–2300 nm) regions are included as model variables. Our results show that during the wet season fibre is better estimated through ecological features that explain the environment (soil type), and plant morphology (plant age and species). Conversely during the dry season when cell water content is negligible, then the SWIR features of lignin and cellulose can be used to predict the concentration of fibre.

Soil type descriptions, significantly explained variations in the phosphorus concentrations in both the wet and dry seasons (Table 4). The soil phosphorus pool is correlated with measured concentrations of foliar phosphorus (Schachtman et al., 1998). Hartshorn et al. (2009) showed the catenal position was associated with variations in phosphorus levels within the soil, supporting the use of the detailed soil classification provided by the South African soil classification system (Macvicar et al., 1977), as this classification system details the catenal soil strata.

For nitrogen, if only environmental variables were considered, then plant age and REP, in addition to species, were significant contributors in both seasons (Table 4). When combining absorption features linked to nitrogen, with the environmental variables, only REP and species remained significant in both seasons. REP, has been associated with nitrogen (Cho and Skidmore, 2006; Gianelle and Guastella, 2007; Mutanga and Skidmore, 2007), but also estimating LAI, plant biomass (Darvishzadeh et al., 2008b; Darvishzadeh et al., 2008a; Gianelle and Guastella, 2007), and in combination with the SWIR region, vegetation condition (Asner et al., 2005). Thus, although REP has been found to be an indicator for forage nutrient concentrations, it has also been linked to plant physical state. When applied to a forage nutrient algorithm, REP should be verified as a variable explaining the forage nutrient variance, and not biomass or plant status.

Findings from earlier studies (Curran, 1989; Darvishzadeh et al., 2008b, 1996; Jacquemoud et al., 1995), showed that bands selected in studies on fresh leaves frequently did not coincide with bands directly linked to the nutrient under investigation. Our studies showed that prediction using only features associated with physical bond vibrations yielded poor predictions of forage component concentrations. The wavelengths (as highest loadings in the PC) attributed to predicting the forage concentrations also varied between seasons. With the addition of ancillary data, to models of physically linked wavelengths, there was a significant improvement in model performances.

What is clear from the findings presented here, is that prediction of nutrients using remote sensing techniques is greatly aided by inclusion of environmental variables. Inclusion of suitable variables not only improves model predictions, but also provides grounds for

creating models that can be generalised temporally. In this study we considered as ancillary data, variables that have been ecologically tied to variations in nutrients. Asner and Martin (2008) and Kokaly and Clark (1999) highlighted remote sensing features that are associated to changes in vegetation structure (water content) and morphology (architecture, leaf area index), and how these optical effects, may influence the detection of biochemicals. Inclusion of such features in combination with environmental variables would provide a logical step for creating generalisable forage nutrient models. In this study we did not analyse for any spatial relationships within the different forage components. A study by Cheng et al. (2007) showed spatial dependence of nitrogen and phosphorus plant nutrients at short ranges (between 47–80 cm ranges) in five grass dominated vegetation communities. It would be expected that such spatial properties exist within these systems and therefore a valuable follow on to this study would be to create a sampling scheme that would allow for such analysis to take place, and determine if there are multiple ranges of spatial dependence.

In terms of creating generalisable algorithms for predicting forage component concentrations in savanna grasses, this research showed that, while a base algorithm can be defined for each forage component, additional variables should be included in the wet and dry season if accurate (i.e. where accuracy is defined as above 70% of variation explained) estimations are required. In this study we focused only on grass forage, in savanna systems there is a mixed tree-grass layer, therefore when upscaling to landscape scale with imagery it would be necessary to take into account the tree layer, this could be performed prior to model inversion through a method such as binary slicing (Skidmore et al., 2010), or through utilising the spectral value ranges used in training the model at the time of model inversion (Knox et al., 2011).

The method outlined here can potentially be generalised to other ecosystems but would require the identification of environmental variables that are relevant to these ecosystems. In order to apply the method to generate landscape scale forage quality maps in heterogeneous landscapes would require sensors of both high spectral and spatial resolution. Considering these spectral and spatial requirements there are currently limited sensors available with this capability. Examples of such sensors include the Carnegie Airborne Observatory (CAO), HyMAP sensor, perhaps Airborne Visible/Infrared Imaging Spectrometer (AVIRIS), however the spatial resolution is rather coarse for mapping of heterogeneous grasslands, or for very high resolution mapping the use of Unmanned Airborne Vehicles (UAV).

Although this linear regression method is an attractive and simple approach to implement, we believe the following aspects need further consideration:

1. Error propagation is a factor which has not been considered here, but could have implications for the stability of model outcomes. With each created data layer, there is a certain level of uncertainty attached to it, e.g. the possibility of a misclassification of a species, or perhaps a geological boundary shift. Thus with the inclusion of data into the modelling of biochemicals there is a need to critically assess the quality of the data.
2. A second aspect for consideration is the selection of the appropriate data layers. In this study for example we decided to use a fire layer based on the frequency of burns over a time interval, a feature shown to influence vegetation structure (Levick et al., 2009). The effect of fire on savannas is complex, and it might well be that a more appropriate layer could be fire intensity, or time since last fire (van de Vijver et al., 1999; Knox et al., 2011).
3. A spectrum taken of vegetation, not only captures the physical contents of the plants, but also aspects of plant structure. In using environmental variables for modelling, there needs to be an assessment of the relationship between these variables to other plant physical variables measured in a spectrum, e.g. LAI or biomass.

5. Conclusion

In this study our main findings were:

1. Combining ancillary and absorption data for mapping of forage nutrients in savanna produces ecologically sensible outcomes with high predictive capabilities in both dry and wet seasons.
2. Species and categorical soil classifications were two ecological variables that repeatedly (temporally and between forage components) significantly contributed to the estimation of forage quality.
3. Ancillary data could model forage component concentrations with higher goodness of fit and prediction outcomes in both the wet and dry seasons, than absorption data alone.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.isprsjprs.2012.05.013.

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