OBSERVING TEMPORAL AND SPATIAL VARIABILITY OF FORAGE QUALITY

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List of Acronyms

ADF acid detergent fibre

AIC Akaikes information criteria

ANN artificial neural networks

ARC Agricultural Research Council, Nelspruit

ASD Analytical Spectral Devices, Inc.

ASTER Advanced Spaceborne Thermal Emission and Reflection Radiometer

CAI cellulose absorption index

CAO Carnegie Airborne Observatory

CRR continuum removed reflectance

GER Geophysical Environmental Research corp.

FOV field of view

IFOV instantaneous field of view

LAI leaf area index

LOO leave-one-out cross validation

KNP Kruger National Park

NDVI normalised difference vegetation index

NDWI normalised difference water index

NIR near infrared (700–1400 nm)

NIRS near infrared spectroscopy

NLV number of latent variables

nPA without plant age

PA plant age

PCR principal component regression

PhIX phenological index

PLS partial least squares

PLSR partial least squares regression

PRESS prediction residual error sum of squares

REP red edge inflection point

RMSE root mean square error

RMSEP root mean square error of prediction

RS remote sensing

sMLR stepwise multiple linear regression

SNR signal-to-noise ratio

SWIR shortwave infrared (1400–3000 nm)

SWIR2 shortwave infrared 2 (2000–2300 nm)

VNIR visible near infrared (400–1400 nm)

Abstract

Forage nutrients vary both spatially and temporally. Imaging spectroscopy studies have shown that it is possible to map various forage nutrients. These studies have focussed on discerning the spatial variation of nutrients in the wet season. In savanna systems grazing herbivores rely on the grass resource for their sustenance. During dry seasons the quality of the grazing resource declines often to within and below critical limits for maintenance. For rangeland managers it is therefore of importance that quality can be assessed in both the wet and dry seasons. With the use of a greenhouse experiment, field studies and an image acquisition, it has been shown in this study, that it is possible to observe variability in the quality of the grazing resource (expressed as concentrations of nitrogen, phosphorus and fibre) both spatially and temporally.

Changes in vegetation between the wet and the dry season resulted in different spectral and ancillary (ecological) variables being selected in the forage quality models. This means that developing a single model for each nutrient, that can be applied irrespective of season, is apparently not feasible. However, within a season it appeared that certain wavelengths were consistently selected (e.g. for nitrogen in the wet season absorption features at 640, 910 and 1020 nm were repeatedly selected). In terms of ancillary variables, the physiology of a grass (captured as species and\or age) and soil type were found to be significant variables that contribute to models estimating grass quality in both the wet and dry seasons.

Models developed in a heterogeneous field environment (Northern Plains of the Kruger National Park, RSA), in the wet and dry seasons for the three forage nutrients, achieved results which explained between 49%–74% of the forage quality variability. Combining spectral and ancillary (spatially derived ecological variables) variables into forage quality models aided upscaling from laboratory $\rightarrow$ field $\rightarrow$ airborne level, making it possible to analyse spatial variations in forage quality nutrients. From laboratory $\rightarrow$ field upscaling it was shown that, at least with nitrogen, masking of features by prominent plant biochemicals (e.g. water and photosynthetic pigments) influenced the selection of absorption features.

Through linear modelling applied to analyse the three forage nutrients, it was found that absorption features in the SWIR region were prominent when ancillary variables were included. A non-linear modelling approach using only the VNIR spectral range achieved comparable, but slightly inferior results. Non-linear models typically achieve higher accuracy models compared to linear models, implying that forage nutrient mapping ideally require a full spectral (VNIR–SWIR) range sensor.

The output from this study provides a valuable contribution to the field of nutrient mapping, and rangeland management in savanna or grassland environments. It has been shown that in an ecologically sensible way, it is possible to observe both temporal and spatial variations of forage quality.

Acknowledgements

Attending the PE&RC weekend back in 2005, I smirked at the idea of a PhD taking more than four years, let alone the Dutch average of 5.2 years. Sitting here, rapidly approaching the 5.2 year mark, I wonder what happened with all this time. In finally achieving the scientific endeavour, that culminates in this thesis, the years have flown by. During this time I have learnt and experienced so much, both on an academic and a personal level, and I would like to acknowledge a number of people and institutions that have assisted me along this memorable journey.

The frequently quoted phrase "money makes the world go round", is strikingly evident within the research world where access to finance, and intensive competition for available funding seems to make or break young scientists. I would like to thank NWO-WOTRO (funding made available through under this project: w.01.53.2004) and ITC for their support of scientific research, and in particular for the financial support awarded to me to allow me to complete this PhD research.

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Herbert, at the start of this research, I believed I would be more extensively collaborating with REG in terms of understanding the role of forage quality in herbivore movements. This did not come to fruition as my study focused primarily on the remote sensing science of forage quality detection, so in this respect I know I have not truly benefited from the wealth of your knowledge. I really appreciated your critical and thorough insights when reviewing my work, thank you.

In the first years of my PhD, during the greenhouse experiment, and later when returning from the field for my chemical analysis, I really had the pleasure of getting to know and working with a number of very special people in the WUR-REG team. Anne-Marie, bedankt voor al jouw hulp in het laboratorium. Het was altijd leuk om met jou en de groep te praten, bij de koffie, of tijdens skeeleren. I was really lucky to have made some wonderful friends on my visits to Wageningen, Anna, Ignas, Nicol, Yvonne, Alejandra and fellow TEMBO'ers. It always made coming to Wageningen a rewarding time, because not only was I able to enjoy doing lab or course work, but I could also enjoy spending time with friends. Nicol, Ale and Anna, thank you for opening up your homes (and floors) for me to crash on!

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Doing my fieldwork, in the KNP, had 2 advantages: not only did I get to work in KNP, but it also gave me the chance to see family and friends during my studies. I find it difficult to imagine how I could have successfully carried out my fieldwork and PhD without the incredible support of my family. Thank you all so much for not only assisting me with logistic support (cars, laptops, airport pick-ups, etc..), but also mental support with phone calls, e-mails, jokes and words of encouragement throughout.

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Chapter 1

Introduction

1.1 Forage nutrients in African savanna systems

Globally savanna and grassland systems sustain a wide diversity of grazing herbivores [Jones and Wilson, 1987]. In these ecosystems, the energy available for herbivore metabolism (e.g.,maintenance, lactation) is a function of the quantity and quality of the forage resource. The importance of these ecosystems for maintaining not only wild ungulates, but also domestic livestock, has lead to extensive research into the quantification of the forage resource.

In an effort to obtain, at minimum, maintenance levels, it is necessary for a herbivore to obtain both energy and nutrients from their food source [Prins and van Langevelde, 2008a]. In African savannas, forage is often limited by either nitrogen or phosphorus, or co-limited by both these nutrients [Grant and Scholes, 2006; McNaughton and Banyikwa, 1995]. Forage fibre concentrations, tend to be high in these systems, in comparison to temperate systems [Jones and Wilson, 1987]. Forage quality is traditionally described in terms of either fibre concentration alone, or both nitrogen and fibre concentrations. In systems where co-limitation from phosophorus also occurs, ideally all three nutrients should be considered when evaluating forage quality.

Studies into variations in nutrient concentrations in tropical ecosystems, have determined numerous factors that are linked to observed differences in the forage resource. Within savanna systems nutrients have been shown to differ significantly between seasons [Grant et al., 2000; McNaughton, 1987, 1990]. These seasonal differences, in combination with limitation of certain nutrients, have been attributed to the mass migrations of herbivores observed in East Africa [McNaughton, 1990]. Variations in nutrient concentrations have been linked to biotic factors such as plant species [Jones and Wilson, 1987; McNaughton, 1988; Mutanga et al., 2004b; Seagle and McNaughton, 1992], phenological development [Jones and Wilson, 1987; McNaughton, 1988], below and outside tree canopies [Treydte et al., 2007, 2008], and grazing [Archibald, 2008; Augustine, 2003]. Abiotic factors have included soil [Allred and Snyder, 2008; Craine et al., 2009; Heitkönig and Owen-Smith, 1998], geology [Grant and Scholes, 2006; Ferwerda et al., 2006a], topography [Seagle and McNaughton, 1992]; and anthropogenic factors such as fire [Allred and Snyder, 2008; van de Vijver et al., 1999], and fertilisation [Jones and Wilson, 1987]. The interaction of these different

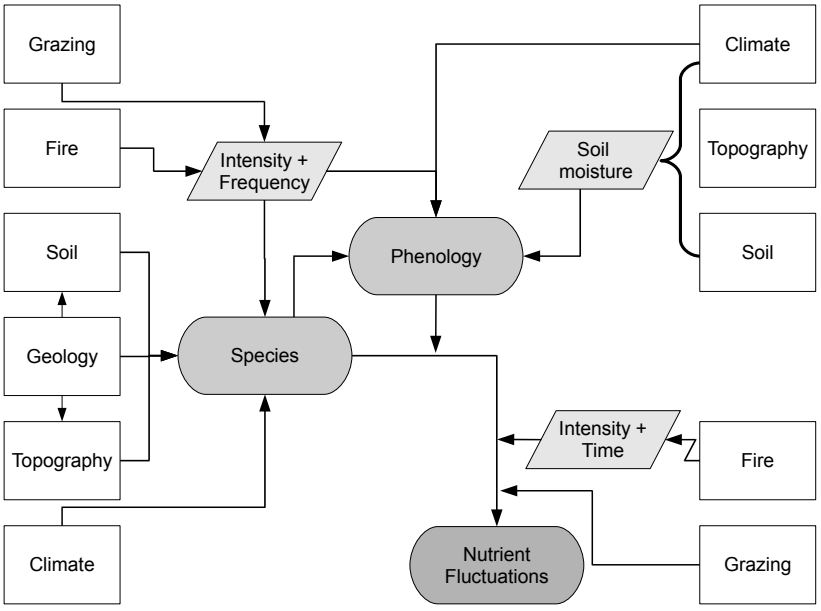

Figure 1.1: Depiction of the interaction of ecological factors, resulting in observed fluctuations in plant nutrient levels across a savanna system.

ecological factors to create the observed fluctuations of nutrients concentrations across a savanna system is depicted in figure 1.1.

These and similar studies highlight the fact, that at various spatial scales, forage nutrient levels vary. Rangeland management of forage quality is primarily based on point based studies [Mirik et al., 2005]. With such studies it is, however, difficult to assess the nature of the nutrient distribution, e.g. uniform or patchy. Such information would be useful for rangeland managers, in terms of planning rotation times in pastures, or for wildlife managers, to build models to calculate carrying capacity or predict distribution models of game.

The main aim of the research presented in this thesis, is to provide remote sensing techniques that can be used for monitoring forage nutrient concentrations in savanna systems. The savanna system where this study was conducted was located on the Northern Plains of the Kruger National Park, South Africa. As mentioned above, nitrogen and phosphorus are found to

be limiting in African savannas, both of these nutrients, in combination with fibre were considered, for the evaluation of forage quality.

1.2 Remote sensing of forage nutrients

Remote sensing provides a platform for analysing continuous variables over large areas. Multi-spectral sensors, have proved useful in mapping broad biophysical and geological features [Ustin, 2004]. It was, however, the development of imaging spectrometers in the 1980's to early 1990's that paved the way for mapping of biochemicals in vegetation [Asner, 2004]. Biophysical and empirical modelling have been the two approaches followed for investigating the physical and chemical properties of plants [Jacquemoud et al., 1995].

Biophysical models have been successfully used for the determination of physical properties such as leaf area index (LAI), leaf angle distribution (LAD) and chemical properties such as chlorophyll, and water [Jacquemoud et al., 2009]. This modelling approach has been unable to resolve for the range of nitrogen compounds contained in leaves of different species [Kokaly et al., 2009], and is limited in its ability to invert models in heterogeneous grassland systems [Darvishzadeh et al., 2008a]. The use of empirical modelling for biochemical modelling has it foundation in near infrared spectroscopy (NIRS). In the 1970's, NIRS provided a theoretical basis for utilising spectroradiometry to discern biochemical features [Starks et al., 2004].

Initial NIRS studies were aimed at developing techniques to rapidly assess forage quality, for agricultural purposes [Clark, 1989]. Through NIRS studies absorption features associated with forage nutrients were identified [Curran, 1989; Fourty et al., 1996; Himmelsbach, 2000]. In this research I have focussed on the use of empirical modelling for the determination of plant biochemicals. The modelling approaches applied here have used, as their foundation, known absorption features linked to forage nutrients. In table 1.1, the location of absorption features, linked to the forage nutrients, nitrogen (protein and nitrogen) and fibre (cellulose and lignin), and their associated physical properties are listed. Unlike nitrogen and fibre, linking phosphorus to absorption features in plant molecules is more challenging. Within plants, the concentration of phosphorus is much lower than either

nitrogen (10 times lower), or fibre (up to 100 times lower). This low concentration will reduce the ability to directly detect phosphorus through spectral signatures, therefore associated links are made with respect to plant activity. Within plants, phosphorus is primarily associated with plant metabolic processes. In this thesis, spectral links to phosphorus concentrations are made through associating phosphorus to sugars and starches, as products of metabolism. These absorption features are also presented in table 1.1.

Table 1.1: Absorption features related to physical bond vibrations of forage nutrients, compiled from the following texts: Curran [1989]; Fourty et al. [1996]; Himmelsbach [2000] and Kumar et al. [2001].

λ **(nm)**	**Bond vibrations**	**Biochemical**
430	electron transition	chl a
460	electron transition	chl b
640	electron transition	chl b
660	electron transition	chl a
910	$C-H$ stretch, 3^{rd} overtone	protein
970	$O-H$ bend, 1^{st} overtone	water, starch
990	$O-H$ bend, 2^{nd} overtone	starch
1020	$C-H$ stretch, 2^{nd} overtone	protein
1120	$C-H$ stretch, 2^{nd} overtone	lignin
1200	$O-H$ bend, 1^{st} overtone	water, cellulose, starch, lignin
1420	$C-H$ stretch, $C-H$ deformation	protein, lignin
1450	$O-H$ stretch, 1^{st} overtone, $C-H$ stretch and deformation	starch, sugar, lignin, water
1490	$O-H$ stretch, 1^{st} overtone	cellulose, sugar
1510	$N-H$ stretch, 1^{st} overtone	protein, nitrogen
1530	$O-H$ stretch, 1^{st} overtone	starch
1540	$O-H$ stretch, 1^{st} overtone	starch, cellulose
1580	$O-H$ stretch, 1^{st} overtone	starch, sugar
1690	$C-H$ stretch, 1^{st} overtone	protein, nitrogen, lignin, starch
1730	$C-H$ stretch	protein, cellulose, lignin
1780	$C-H$ stretch, 1^{st} overtone, $O-H$ stretch, $H-O-H$ deformation	cellulose, sugar, starch
1820	$O-H$ stretch, $C-O$ stretch, 2^{nd} overtone	cellulose

Continued on next page...

Table 1.1 (Continued)

λ (nm)	Bond vibrations	Biochemical
1900	$O-H$ stretch, $C-O$ stretch	starch
1940	$O-H$ stretch and deformation	protein, nitrogen, lignin, starch, water, cellulose
1950	$O-H$ stretch and deformation	protein, nitrogen, lignin, starch, water, cellulose
1960	$O-H$ stretch and bend	protein, sugar, starch
1980	$N=H$ asymmetry	protein, lignin
2000	$O-H$ deformation, $C-O$ deformation	starch
2060	$N-H$ bend, $N-H$ stretch, 2^{nd} overtone	protein, nitrogen
2080	$O-H$ stretch and deformation	sugar, starch
2100	$O=H/C-O$ stretch, $C-O-C$ stretch, 3^{rd} overtone	starch, cellulose
2130	$N-H$ stretch	protein
2180	$N-H$ bend, 2^{nd} overtone, $C-H$ stretch, $C-O$ stretch, $C-N$ stretch	protein, nitrogen
2240	$C-H$ stretch	protein
2250	$O-H$ stretch and deformation	starch
2270	$C-H$ stretch, $O-H$ stretch, CH_2 bend, CH_2 stretch	protein, nitrogen, lignin, starch, sugar,cellulose
2280	$C-H$stretch, CH_2 deformation	starch, cellulose
2300	$N-H$ bend, $C-O$ stretch, $C-H$ bend, 2^{nd} overtone	protein, nitrogen, cellulose
2320	$C-H$ stretch, CH_2 deformation	starch
2340	$C-H$ stretch and deformation, $O-H$ stretch and deformation	cellulose
2350	CH_2 bend, 2^{nd} overtone, $C-H$ deformation, 2^{nd} overtone	protein, nitrogen, cellulose

Remote sensing studies of biochemicals in vegetation has been a stepwise procedure. Studies have not been confined to a single ecosystem or a single nutrient, although, comparatively, nitrogen has been extensively researched. The first studies identified significant wavelengths that predicted the concentration of nutrients in dried and ground material [Card et al., 1988; Grossman et al., 1996]. This progressed onto studies on fresh leaves [Curran et al., 1992, 2001; Grossman et al., 1996], then onto fully canopies of either single or multiple species [Asner, 1998; Darvishzadeh et al., 2008c; Johnson et al., 1994; Martin and Aber, 1997; Martin et al., 2008; Mutanga

et al., 2004c; Peterson et al., 1988; Serrano et al., 2002], and finally generating maps of nutrient concentrations from hyperspectral images across landscapes [Martin and Aber, 1997; Mutanga and Skidmore, 2004a; Mutanga and Kumar, 2007; Skidmore et al., 2010; Wessman et al., 1988].

In the biochemical studies listed above, a recurrent finding, was that selection or identification of all the spectral features did not coincide with features that had been physically linked (through bond vibrations, e.g. like those listed in table 1.1) to the biochemical under observation. Features were often linked to other nutrients [Johnson et al., 1994], or explained in terms of plant or spectral properties [Asner, 1998; Grossman et al., 1996; Jacquemoud et al., 1995]. A couple of attempts to generalise biochemical models between sites has had limited success [Martin and Aber, 1997; Martin et al., 2008], a result most likely attributed to the inclusion of "non-physically" linked absorption features. In order to create a model that can be generalised between sites or temporally, model variables should exclude site or temporal specific data. As an example, a generalised biochemical model that can be applied at multiple sites should contain only biophysical variables associated to variations in the nutrient of interest, e.g. absorption features for that nutrient, LAI, phenology, and water content, and should exclude site specific variables, e.g. species, or soil layer.

Temporal factors play an important role in nutrient models. There is *a-priori* knowledge that nutrients fluctuate between seasons, and that concentrations alter with respect to plant age [Grant et al., 2000; Jones and Wilson, 1987; McNaughton, 1988, 1990]. From a remote sensing perspective, it is known that optical properties of plants alter with ageing [Asner, 2004]. Understanding the role of time (season and plant age) in biochemical mapping, would provide a valuable contribution towards the task of creating a repeatable means for nutrient mapping.

Studies within the focal savanna system have shown that, particularly in the dry season, the concentrations of forage often fall below maintenance level requirements of herbivores [Grant et al., 2000; Grant and Scholes, 2006; Treydte et al., 2009]. In biochemical remote sensing studies, there has been an emphasis placed on the peak growing season, and limited emphasis on the senescent stage of vegetation. In order to provide remote sensing techniques that can be used to monitor biochemical concentrations in vegetation, with an emphasis on forage, it was considered, that the influence of plant ageing and seasons in this process should be investigated.

1.3 Research objective

The main objective of the research presented here, is to provide a technique for spatially and temporally monitoring forage quality in an African savanna system. To achieve this the role of seasonal and plant age influences in biochemical mapping were investigated. The means, and structure taken to investigate these objectives is described below.

1.4 Outline of the thesis

This thesis is a compilation of seven chapters. Besides the introduction and synthesis, the five remaining chapters are in preparation or have been submitted, to the scientific peer review process. The structure and content used in submitting the manuscripts is largely retained in the thesis.

The research was conducted in three stages, a greenhouse-laboratory level, this was scaled up to a field level and finally an application using airborne imaging spectroscopy.

1.4.1 Greenhouse-laboratory level

A greenhouse study provided the opportunity, in a controlled environment, to investigate plant ageing effects on biochemical predictions, with the utilisation of spectroradiometry.

Chapter 2:

Given the theoretical basis for biochemical mapping was founded in NIRS, in this chapter, it was investigated how procedures applied to NIRS biochemical studies, upscaled to field spectroscopic studies. Using plant nitrogen as the basis for this study, the investigation captured the differences in how sample preparation for laboratory and field studies influences spectroscopic nutrient modelling.

Chapter 3:

Changes in plant phenology are primarily driven by climatic changes, but at local scales plant age differs between plants as a result of micro - topographical differences (e.g. soil moisture and catenal position) [Archibald and Scholes, 2007]. Plant phenology has been empirically associated with nutrient fluctuations [Jones and Wilson, 1987; McNaughton, 1988], and thus its effect on predictive models, for forage nutrient concentration estimation, should ideally be understood when building remote sensing - nutrient prediction models. In chapter 3, of this thesis, the integration of plant age into models for predicting forage nutrient concentrations utilising spectroradiometry, was investigated.

Chapter 4:

In chapter 3, plant age was a co-variate variable, generated from the experimental design, and thus each age defined was known prior to analysis. Across an image covering a savanna system, the phenological condition of plants would differ, with variations in topography. The findings from chapter 3 indicate that inclusion of a variable that captures variation in plant ageing, is beneficial for nutrient mapping. In chapter 4, a comparison is made of indices that have been used for determining vegetation condition, in addition to the presentation of a new phenological index. Indices that could statistically separate age classes, in chrono-sequence of the plants age, were evaluated against data collected in the field.

1.4.2 Field level

Chapter 5:

Ecologists have identified numerous variables that explain forage nutrient variability (depicted in figure 1.1). Spectroscopically, research has identified absorption features that are physically associated with each of the individual forage nutrients (table 1.1). In chapter 5 of this thesis, the findings of earlier ecological and spectral research are combined, to test if together this information can be used to create reproducible monitoring models for

predicting forage nutrients in savannas, irrespective of seasons.

1.4.3 Airborne level

Chapter 6:

Findings from the field and laboratory level studies provide evidence that mapping of forage nutrients is possible irrespective of season and plant age. In chapter 6, the findings from earlier chapters are combined and upscaled through to image data. For the first time, forage nutrients in savanna systems are mapped during the dry season. The findings observed in the nutrient distribution maps, are considered in terms of relationships through to the savanna environment under evaluation.

The research presented here combines aspects of both a technical nature, in terms of applied remote sensing, and a theoretical ecological nature. In the final chapter of this thesis (chapter 7), the findings of this study are considered in terms of the contributions made to the field of image spectroscopic science for biochemical mapping. Caveats are identified and suggestions towards further research are presented.

Chapter 2

Upscaling nutrient prediction models, from dried - to canopy plant material*

*This chapter is based on the following paper: Knox, N.M., Skidmore, A.K., Schlerf, M., de Boer, W.F., van Wieren, S.E., van der Waal, C., Prins, H.H.T. and Slotow, R. 2010. Nitrogen prediction in grasses: Effect of bandwidth and plant material state on absorption feature selection. *International Journal of Remote Sensing* 31, 691–704.

Abstract

We analysed stability and predictive capabilities of known nitrogen absorption features between plant material prepared for NIRS (dried) and RS (fresh) studies. Grass spectra were taken of the plant canopy, and again after the grass sample was dried and ground. Models were derived using stepwise multiple linear regression (sMLR). Regression values (R^2_{adj}) produced using the dried material, were greater than those produced using canopy material. For dried material only wavebands from the SWIR region were selected. Wavebands selected by sMLR on canopy material were located in both the VNIR and SWIR regions. Using wavebands selected for dried material models produced low R^2_{adj} values when applied to canopy plant material, differences in R^2_{adj} values are smaller when wavebands selected in canopy material models are applied to dried material. Widening of nitrogen features produced higher R^2_{adj} values for both dried and canopy material. This work shows that obtaining models with high predictive capabilities for nitrogen concentration is possible, but waveband selection should not be limited to features identified by NIRS studies. To accommodate for variability in absorption features, and instrument errors, absorption features should be widened.

2.1 Introduction

The ability to map biochemicals provides the opportunity to investigate nutrient fluxes, system productivity, and provide input into models analysing ecosystem processes. Mapping of biochemicals through remote sensing (RS) has followed two principle approaches, physically based modelling [Darvishzadeh et al., 2008a; Schaepman et al., 2005; Gastellu-Etchegorry and Bruniquel-Pinel, 2001; Jacquemoud et al., 2000] and empirical approaches [Chen et al., 2007; Mutanga and Skidmore, 2007; Huang et al., 2004; Mutanga et al., 2004c; Curran et al., 1997; Johnson and Billow, 1996; Jacquemoud et al., 1995]. The empirical approach, which is the focus of this study, has developed closely with near infrared spectroscopy (NIRS).

Initial vegetation NIRS studies were focused on developing techniques to rapidly assess the quality of vegetation for agricultural purposes [Clark, 1989]. Through the use of NIRS, numerous absorption features were found

to relate biochemicals to electron transitions, and bond vibrations. The application of NIRS for the analysis of vegetation quality has become a standard technique applied by the US agricultural board [Marten et al., 1989; Barton II and Windham, 1988]. The standard NIRS method measures spectra on dried ground material.

Unlike NIRS, remote sensing, when applied to vegetation, has to consider the influence of fresh canopy vegetation, e.g. leaf water content and canopy structure, and the implications of distance from subject, e.g. atmosphere, soil background and signal-to-noise ratio (SNR), on spectra [Peterson and Hubbard, 1992]. Biochemical spectroscopic studies have been extended from NIRS to remote sensing, with varying degrees of success. These studies have attempted to determine wavelengths and spectral features that relate to the biochemicals of interest, the selected wavelengths are then checked to see if they relate to features that have been previously identified as absorption features using NIRS. Biochemical measurements have been made on fresh leaves [Grossman et al., 1996; Curran et al., 1992; Card et al., 1988] as well as plant canopies - single and multiple species [Darvishzadeh et al., 2008c; Martin et al., 2008; Mutanga et al., 2004c; Serrano et al., 2002; Asner, 1998; Martin and Aber, 1997; Johnson et al., 1994; Peterson et al., 1988; Wessman et al., 1988].

Biochemical concentrations within plants alter with age and over seasons. Nutrients move to different areas of the plant in response to growth, flowering or senescence [Salisbury and Ross, 1992], so it would be expected that these changes are reflected in the spectra. Ideally a model that can predict a biochemical irrespective of plant age or species would allow for seasonal monitoring.

Ecologically many biochemicals are important not only to plant growth, but also to animals that forage on them [du Toit et al., 2003; Provenza, 1995]. Many absorption features, caused by bond vibrations of plant biochemicals, amongst others relate to plant nitrogen concentrations (table 2.1). Given the ecological importance of nitrogen [Prins and van Langevelde, 2008a; Owen-Smith and Danckwerts, 1997], we chose to base our study on this biochemical. The absorption features selected for predicting nitrogen in plants include bonds that have been linked to: Elemental nitrogen; chlorophyll [Yoder and Pettigrew-Crosby, 1995]; protein, which includes nitrogen as an elemental constituent and is an essential component of herbivore diets [Provenza et al., 2003; Provenza, 1995]; and the red edge position which

has been shown to be useful in estimating numerous biophysical variables, including nitrogen concentration [Mutanga and Skidmore, 2007; Cho and Skidmore, 2006].

Although many studies using fresh material have included wavelengths identified by NIRS on dried material [Cho and Skidmore, 2006; Mutanga, 2004; Huang et al., 2004; Serrano et al., 2002; Martin and Aber, 1997; Curran et al., 1997; Johnson et al., 1994; Matson et al., 1994], no study that we are aware of, has explored how stable known spectral absorption features are between the same plant samples measured as both fresh canopy, and then dried and ground. We investigated whether nitrogen absorption features selected in prediction models of dried plant material, from plants of different phenological stages, are preserved in plant canopy models, and vice-versa.

The biochemical spectral studies referenced above have been conducted using a wide variety of spectroradiometric instruments e.g. GER 3700, GER Mark IV, AVIRIS, etc., these instruments differ with respect to their number of wavebands, wavelength centres, band widths and calibration settings. To consider this variation on biochemical predictions we tested the effect of increasing the width of absorption features, on the stability of model variables obtained in dried and fresh plant canopy material.

2.2 Methods

2.2.1 Sample preparation and measurement

In a greenhouse experiment we grew two tropical grass species, *Digitaria eriantha* and *Urochloa mosambicensis*, on soils with three different nitrogen treatments (0.05, 0.125 and 0.2 % N per 1 kg soil). The nitrogen levels in the soil were based on levels found in the Kruger National Park (KNP), South Africa, where both grass species occur as dominant species, and are considered to be important foraging grasses [van Oudtshoorn, 1992]. Pots were placed in a randomized layout. The conditions within the greenhouse were maintained at a constant temperature of 25°C, with 12 daylight hours, and daily watering of the grasses. Three weeks after seed germination the number of grasses within the pots were thinned. To reduce soil background effects at the time of the spectral measurements, sufficient grass plants were

Table 2.1: Absorption features related to plant nitrogen [Cho and Skidmore, 2006; Ferwerda, 2005; Mutanga, 2004; Huang et al., 2004; Serrano et al., 2002; Martin and Aber, 1997; Curran et al., 1997; Fourty et al., 1996; Johnson et al., 1994; Matson et al., 1994; Curran et al., 1992; Card et al., 1988]

λ (nm)	Bond vibrations	Biochemical
430	electron transition	chl a
460	electron transition	chl b
640	electron transition	chl b
660	electron transition	chl a
910[a]	$C-H$ stretch, 3^{rd} overtone	protein
1020[a]	$C-H$ stretch, 2^{nd} overtone	protein
1420	$C-H$ stretch, $C-H$ deformation	protein, lignin
1510[a]	$N-H$ stretch, 1^{st} overtone	protein, nitrogen
1520[a]		protein
1690[a]	$C-H$ stretch, 1^{st} overtone	protein, nitrogen, lignin, starch
1730[a]	$C-H$ stretch	protein, cellulose, lignin
1940	$O-H$ stretch, $O-H$ deformation	protein, nitrogen, lignin, starch, water, cellulose
1950	$O-H$ stretch, $O-H$ deformation	protein, nitrogen, lignin, starch, water, cellulose
1960	$O-H$ stretch, $O-H$ bend	protein, sugar, starch
1980[a]	$N=H$ asymmetry	protein, lignin
2060[a]	$N-H$ bend, $N-H$ stretch, 2^{nd} overtone	protein, nitrogen
2130[a]	$N-H$ stretch	protein
2180[a]	$N-H$ bend, 2^{nd} overtone, $C-H$ stretch, $C-O$ stretch, $C-N$ stretch	protein, nitrogen
2200[a]		protein
2240[a]	$C-H$ stretch	protein
2270	$C-H$ stretch, $O-H$ stretch, CH_2 bend, CH_2 stretch	protein, nitrogen, lignin, starch, sugar,cellulose
2290[a]		protein
2300[a]	$N-H$ bend, $C-O$ stretch, $C-H$ bend, 2^{nd} overtone	protein, nitrogen, cellulose
2350[a]	CH_2 bend, 2^{nd} overtone, $C-H$ deformation, 2^{nd} overtone	protein, nitrogen, cellulose
REPd[a,b]		nitrogen
REPc[a,b]		nitrogen
REPg[a,b]		nitrogen

[a] wavelength shown to relate to nitrogen in fresh material

[b] red edge inflection point (REP), calculated using a standard derivative (REPd), linear four-point interpolation (REPg) and linear extrapolation (REPc), formulae in Cho and Skidmore [2006]

Table 2.2: Phenological classes and numbers of samples included in each class of spectral measurements

Species	Phenological stage	Code	Weeks from sowing	Samples
D. eriantha	Seedling	DES	5	31*
D. eriantha	Adult	DEA	8	38
U. mosambicensis	Adult	UMA	10	27
Spp. combined	Adult & Seedling	All	NA	86

* Only 21 samples were included on the fresh material measurements

kept within each pot to ensure that, at the different phenological stages, the soil would be covered. As the germination rates of *U.mosambicensis* were low, there were only sufficient numbers of germinated seed to be included in a single phenological age, it was decided to measure them at the adult stage, at this phenological stage the plant material was sufficient to cover the soil.

Spectra were measured at two phenological stages: seedling and adult. At the seedling stage, morphologically the *D.eriantha* seedling canopy was a tufted, erect grass standing approximately 15–25 cm high. The adult stages of both *D.eriantha* and *U.mosambicensis* were without flower and reached a height of approximately 70 cm, *U.mosambicensis* formed denser tufts and their leaves were slightly broader than those of the adult *D.eriantha* plants. The number of spectral samples take for each of the phenological stages is presented in table 2.2. Spectra were measured using a GER 3700 spectroradiometer (Geophysical and Environmental Research Corp.). The GER 3700 is a three dispersion grating spectroradiometer using Si and PbS detectors with a single field of view. The instrument has a wavelength range of 350–2500 nm, the spectral range has a resolution of 1.5 nm in the 350–1050 nm range, 6.2 nm in the 1050–1900 nm range and 8.5 nm in the 1900–2500 nm range.

For fresh canopy material (referred to as 'fresh material' hereafter) measurements, the GER 3700 was fitted with a 10° optic, and placed on a tripod at a 15° angle, 80 cm above the pot rim level, creating a field of view (FOV) of 14 cm in diameter (the diameter of the pot size at rim level was 19 cm). Mounting the spectrometer at this height, above the pot rim, allowed for the projected plant growth between a seedling and an adult

growth phase, and ensured that the same setup could be maintained for all phenological stages. The calibration panel (Labsphere, Inc, Sutton, NH), used for converting the relative reflectance to absolute reflectance, was measured at a distance of 31 cm from the optic, thus creating a FOV of 5.5 cm in diameter. The calibration panel was only 225 cm^2, and thus a FOV of this size ensured an accurate reading of the panel. A halogen lamp was placed alongside the GER 3700 at the same level as the optic.

Potted plants were transferred from the greenhouse to the laboratory for measurement. The pot was fixed in place (to ensure the FOV was located above the pot centre) for a group reading, one group reading consisted of a measure of the calibration panel and a set of 5 readings of the sample. In order to reduce directional effects, caused by leaf orientation within the canopy, the pot was rotated by 90°, and the next group reading taken [Cho and Skidmore, 2006; Mutanga et al., 2003]. The 20 spectral readings taken per pot were averaged to obtain a single spectral reading per sample.

Following the fresh canopy material spectral measurement, all the grasses within a pot were clipped at the plant base and dried at 70°C, for 24 hours. The samples were then ground through a 1 mm sieve (these samples are hereafter referred to as 'dried material'). Spectra were measured with the GER 3700, fitted with a 3° optic, 38 cm above the point of measurement, creating a FOV of 2 cm. To reduce reflectance and directional effects, the dried material was placed in a shallow non-reflective bowl on a non-reflective background and the sample leveled. A measurement of a sample was composed of a calibration panel measurement and 5 readings of the sample. The 5 readings were averaged to create a single reading per sample.

After completion of all spectral measurements, all the samples were chemically analysed. Nitrogen was analysed using the wet chemistry Kjedahl technique [AOAC, 1970].

2.2.2 Data Analysis

Data preparation:

The brightness of the dried material reflectance data were greater than that of the canopy spectral data. These brightness differences were a result of the setup of the canopy measurements, where the distances differed between the

sensor to calibration panel and sensor to the target. In the standard NIRS method and in many RS studies, reflectance data are transformed using log 1/Reflectance [Kokaly, 2001; Grossman et al., 1996; Card et al., 1988]. We tested this and other transformations (first and second derivatives) and found that the first derivative best preserved the absorption feature data. The first derivative acts to removes brightness effects, but is known to enhance sensor noise levels within the spectra. As we were comparing dried and fresh material, and differences in brightness were not constant for all phenological stages, we believe the use of the first derivative was optimal because data properties of the absorption features were maintained (and we found no evidence of enhanced noise at these absorption feature locations), and the comparisons between the materials could be made. Given the aim of our study was to focus on absorption features associated to the physical properties of nitrogen and proteins (table 2.1), only wavebands that corresponded with the absorption features listed in the table 2.1 were included in the data analysis.

Model Development:

The data for the regression analyses were maintained in their separate phenological classes (table 2.2). In addition all the data were grouped together (code: ALL) to determine whether a selection of wavebands could predict nitrogen concentration irrespective of plant age or species. In this study we considered a regression model with an adjusted r^2 value of greater than 0.7 to be a suitable model for prediction of nitrogen concentration, an adjusted r^2 value of greater than 0.5 was considered to be unsuitable for prediction of nitrogen concentration, however it could function to show trends.

Nitrogen concentration (obtained from the chemical analysis of the plant samples) was regressed against the individual known absorption features / wavebands derived firstly from the spectral measures on the dried material, and then the fresh material. The regressions were run using stepwise multiple linear regression (sMLR), a standard method applied within NIRS and frequently applied in RS studies [Huang et al., 2004; Kokaly and Clark, 1999; Martin and Aber, 1997; Marten et al., 1989]. Stepwise regression was run in both directions (forward and backward), to ensure the same wavebands were selected via either method. To avoid over-parametrisation, in the backward regression, the maximum number

of wavebands that could be included within a regression fitting was kept below a threshold ($number samples \div 3$), a technique suggested by Crawley [2006]. Given that 26 absorption features were tested (table 2.1), and the sample numbers (table 2.2) for each of the phenological stages was less than that required to test all wavebands at one time (except for the ALL class), model fitting was undertaken iteratively [Crawley, 2006]. A subset of the 26 absorption features was fed into a model, the significant wavebands were selected, this procedure was repeated until all absorption features had been included in the sub-models. This process was repeated with the order of included wavebands randomised and repeated to test that the same wavebands were selected. All the significant wavebands selected from the sub-models were included in a final selection model to determine which of these wavebands, when placed in a single model was still retained as a significant nitrogen concentration predictor.

Regression models were derived separately for both dried and fresh material. To determine whether the plant material state effected the outcomes of the regression or whether a regression remains stable irrespective of plant material state, the wavebands selected for a model (e.g. dried material) were then used to define a new regression model using the same waveband combinations on the second material (fresh material), and vice versa. The differences in the R^2_{adj} values, and the wavebands that remained significant when applied to the counterpart material, were recorded. Should there be no effect of plant material state on the prediction of nitrogen concentration, then we would expect all the regression variables would remain as significant contributors to the prediction of nitrogen, and the R^2_{adj} of the models would be similar (within a range of the original model 0.1).

Feature widening:

We investigated the influence of widening each of the absorption features. By creating an absorption feature that was wider than a single waveband we believe that selected features of a regression would be more robust as white noise inherent in the reflectance data would be cancelled out. The wider features would ideally reduce the effects from measurements taken using any of the multiple field instruments available together with their requirements for frequent calibration and maintenance, due to shifts in sensors and changing sensitivity across spectra, resulting in shifts of ab-

sorption features [Mutanga and Skidmore, 2007; Kokaly, 2001]. A broader absorption feature would be less sensitive to shifts of an absorption feature within a spectrum. A feature was widened by averaging the derivative value across three neighbouring wavebands (i.e. a waveband above and below each absorption feature). The spectral resolution was maintained in the original form obtained from the GER 3700 instrument, thus the width of the widened features differed across the spectrum (in the 350 nm – 1050 nm range a widened feature was 1.5 nm x 3, in the 1050 nm – 1900 nm range the features were 6.2 nm x 3, and in the 1900 nm – 2500 nm range they were 8.5 nm x 3 wide). The method of applying sMLR as outlined in the above section was then applied to these "widened" features.

2.3 Results

Nitrogen concentration is reported as percentage dry weight, and ranged from 2.33% – 5.00%. In this study we attempted to emulate the soil nitrogen contents found in Kruger National Park (KNP), South Africa. Our results for nitrogen percentage found within the grass samples in this study were higher than those we obtained in several separate studies conducted in the KNP and surrounding regions.

When evaluating the overall spectral curves on dried and fresh material certain differences were consistently observed: The effect of water on fresh vegetation spectra is evident particularly when one looks at the known water absorption features. Although these features are not solely linked to water but also linked to other plant biochemicals (e.g. protein, lignin and starch), they were narrower and deeper in the fresh material compared to the dried material (figure 2.1), the water within the fresh material thus modifies these biochemical absorption features. In addition the red edge feature (i.e. the sharp transition, found in fresh vegetation, between the red and near infrared (700–1400 nm) (NIR) region of the spectrum), is altered in the dried when compared to the fresh material, the absorption feature in the red region becomes shallower and the NIR shoulder is no longer sharply defined, but levels off gently towards the NIR plateau (figure 2.1).

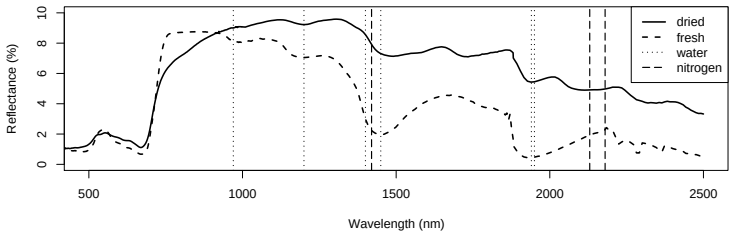

Figure 2.1: Spectra of dried and fresh material for a plant sample with mean (3.871%) nitrogen concentration. The locations of the principal water absorption bands (water) and the three regressors (nitrogen) having the highest correlation with the dried plant samples are shown. Reflectance values of the dried sample were adjusted down by a factor of 8 to account for the increased brightness in this measurement (section 2.2.2).

2.3.1 Narrow absorption feature models

We investigated whether any single waveband consistently predicted nitrogen concentration, irrespective of phenology or the preparation state of material, and found none of the absorption features, that we were considering in this study, consistently had an R^2 value above 0.5 for both dried and fresh material. For the dried material, wavebands centred at 1420 nm, 2130 nm, and 2180 nm (indicated on figure 2.1) were the highest individual predictors (R^2 values greater than 0.5), for all phenological classes.

Absorption features selected by sMLR for the dried material produced prediction performances (R^2_{adj}) above 0.7 (and thus suitable predictive models) for all phenological classes. Almost all selected wavebands for dried material fall within the shortwave infrared (1400–3000 nm) (SWIR) region. These selected wavebands when applied to fresh material, of the same phenological class, have little to no predictive power. The red edge - linear four point interpolation feature (REPg) in the *D. eriantha* adult (DEA) class is the only feature to remain significant, all other wavebands are non-significant contributors to predicting nitrogen concentration in fresh material (table 2.3).

The predictive power (R^2_{adj} values) of models selected by sMLR for fresh material are lower when compared to those models selected for dried ma-

Table 2.3: Wavebands selected and adjusted R^2 values obtained from applying stepwise MLR to dried plant material. These selected wavebands are then applied to the fresh material to determine their ability (R^2_{adj}) to predict on material of the same age, but different preparation state

Selected wavebands (nm)	Age (Code)	Dried Material (R^2_{adj})	Fresh Material (R^2_{adj})
1420, 1690, 2130, 2180	All	0.75	-0.02
1020, 1980, 2200	DES	0.76	-0.01
1420, 2350, REPg*	DEA	0.82	0.12
1980, 2060, 2130, 2300	UMA	0.70	0.14

* wavebands significant when applied to fresh material

Codes: All plant samples grouped (All), D. eriantha seedling (DES), D. eriantha adult (DEA), U. mosambicensis adult (UMA)

Table 2.4: Wavebands selected and adjusted R^2 values obtained from applying stepwise MLR to fresh plant material. These selected wavebands are then applied to the dried material to determine their ability (R^2_{adj}) to predict on material of the same age, but different preparation state

Selected wavebands (nm)	Age (Code)	Fresh Material (R^2_{adj})	Dried Material (R^2_{adj})
640*, 1420*, 2290^c, REPd^c, REPc^c	All	0.53	0.62
910^c, 1940, 1980*^{c}	DES	0.80	0.24
1690^c, 2200^c, 2290^c, REPg*^{c}	DEA	0.43	0.41
1520*^{c}, 1940*, 2240^c	UMA	0.51	0.28

* wavebands significant when applied to dried material

^{c} wavelengths in a previous study related to nitrogen in fresh leaves (table 2.1)

Codes: All plant samples grouped (All), D. eriantha seedling (DES), D. eriantha adult (DEA), U. mosambicensis adult (UMA)

terial. When the wavebands selected for predicting nitrogen for fresh material were applied to dried material, of the same phenological stage, the differences in the R^2_{adj} values is lower than that seen when the situation is reversed (tables 2.3 vs 2.4). More of the fresh material wavebands are significant predictors when applied to the dried material (table 2.4).

We earlier highlighted that there was no single waveband that could predict nitrogen irrespective of the phenology, species or preparation state, how-

ever, we found that at least one of the wavelengths selected in each of our models was solely related to the biochemicals nitrogen or protein (i.e. many features presented in table 2.1 refer to multiple biochemicals). Although *U. mosambicensis* was phenologically an adult plant, in selection of wavebands within the models (fresh/dried), it shared at least one featured waveband (1940 nm in fresh material and 1980 nm in dried material) with the seedling stage of *D. eriantha*, and none with the adult stage of *D. eriantha*.

The results from the narrowband absorption features highlight that models for predicting nitrogen concentration can be obtained for all phenological classes in dried material, but not for fresh material. With narrowband absorption features the state of plant material effects regression variable selection and particularly with models derived from dried material it is not possible to apply the same waveband selections to spectra from fresh material.

2.3.2 Widened absorption feature models

When the wavebands were widened, and the number of wavebands selected in the sMLR's remained unchanged (i.e. not for the DEA class on dried material), the ability to predict nitrogen concentration in models was improved (through an increase in the adj r^2 values) in both the dried (column three in tables 2.5 vs 2.3) and the fresh (column three in tables 2.6 vs 2.4) material.

In comparing the output from sMLR's run on each phenological stage in the narrow absorption features (tables 2.3 and 2.4) and widened features (tables 2.5 and 2.6); when the wavebands selected in widened models were applied to their material counterpart (i.e. when the same wavebands selected from a fresh material model are used with the wavebands from the dried material spectral data, and vice versa), the results again showed that the prediction of nitrogen concentration is affected by plant material state. Creating a widened absorption feature reduced the differences between the between the materials (smaller differences between R^2_{adj} values within each phenological class and increased number of significant values - particularly for the fresh material models then applied to dried material (table 2.6)), in addition the widened absorption features generated better fitting models (higher R^2_{adj} values). The increase in significant predictors carried over between the fresh

Table 2.5: Waveband centres selected and the adjusted R^2 values obtained for widened features selected from stepwise MLR applied to dried plant material. These selected widened wavebands are then applied to the fresh material to determine their ability (R^2_{adj}) to predict on material of the same age, but different preparation state

Selected waveband centres (nm)	Age (Code)	Dried Material (R^2_{adj})	Fresh Material (R^2_{adj})
640, 1940, 2130, 2290*	All	0.77	0.37
1020, 1960, 2200	DES	0.77	0.06
1420, REPg*	DEA	0.79	0.25
1420, 2130, 2300	UMA	0.70	0.34

* wavelengths significant when applied to fresh material

Codes: All plant samples grouped (All), D. eriantha seedling (DES), D. eriantha adult (DEA), U. mosambicensis adult (UMA)

to the dried material models indicate that the wider absorption features are better preserved between these two different plant material states.

Generally the wavebands selected by widening the features altered from those wavebands selected by sMLR on the narrow absorption waveband models. For the dried material wavebands selected by most of the models shared some but not all of the wavebands (tables 2.3 and 2.5). For the fresh material some of the wavebands were selected by both the widened and narrow features, particularly for the *D. eriantha* seedling (DES) class (tables 2.4 and 2.6).

2.4 Discussion

The pronounced differences to the spectral signatures in dried and fresh material (figure 2.1), particularly caused by water, highlight the need to consider features less influenced by the presence of water in the plant material when developing algorithms for biochemical prediction.

Table 2.6: Waveband centres selected and the adjusted R^2 values obtained for widened features selected from stepwise MLR applied to fresh plant material. These selected widened wavebands are then applied to the dried material to determine their ability (R^2_{adj}) to predict on material of the same age, but different preparation state

Selected waveband centres (nm)	Age (Code)	Fresh Material (R^2_{adj})	Dried Material (R^2_{adj})
640*, 1510^c, 1940*, 1950*, REPc*^{c}	All	0.63	0.40
910*^{c}, 1940, 1980*^{c}	DES	0.84	0.34
640*, 1980*^{c}, 2060*^{c}, 2200^c, REPg^c	DEA	0.55	0.68
1020^c, 1420*, 1940, 2290*^{c}	UMA	0.66	0.62

* wavelengths significant when applied to dried material

^{c} wavelength in a previous study related to nitrogen in fresh leaves (table 2.1)

Codes: All plant samples grouped (All), D. eriantha seedling (DES), D. eriantha adult (DEA), U. mosambicensis adult (UMA)

2.4.1 Narrow absorption feature models

The predictive capabilities of models are greater when applied to plant material that has been dried and ground. The selected wavebands in dried material have little to no predictive capabilities when applied to fresh material. The wavebands selected for dried material differ from those wavebands selected for models built using fresh material (column 1 in tables 2.3 and 2.4). Our study shows that absorption features selected in dried plant material are not preserved in fresh canopy material.

Wavelengths selected by models built using dried material (table 2.3) are almost exclusively located within the SWIR (1400 nm – 3000 nm) region, in contrast wavelengths selected on fresh material (table 2.4) include wavelengths located in both the visible near infrared (400–1400 nm) (VNIR) and SWIR regions, a result in agreement with Jacquemoud et al. [1995]. For dried material, in each phenological stage, a wavelength was selected that is linked to a 2^{nd} overtone bond vibration (table 2.1), though Curran [1989] suggested that these wavelengths were hidden by sensor noise in field and airborne sensors. These wavelengths were not selected for the fresh material models, indicating that these wavelengths might also be influenced by

the canopy and leaf structure of the plant.

Spectral measurements on plant canopies are affected by several factors: leaf structure (thickness, cell structure), plant symmetry (which includes leaf orientation), leaf area and background. In this experiment we dealt with only a single plant functional group (grasses), and thus the leaf structure was consistent through the analysis. The rotation of the pot between measurements and averaging the spectra would account for plant symmetry effects. We therefore managed to keep as constants in the measurements the leaf structure and plant symmetry, the leaf area and the soil background are however still factors that would influence the prediction capabilities for biochemicals in the analysis of fresh canopy material. Leaf area (measured in remote sensing as the LAI (LAI - that is the ratio of the total one sided leaf area per unit ground surface area) would not have been constant across all the plant canopies in each of the measurement stages. In our study, for each measurement stage, we felt that the variations in LAI would have been negligible given that the plants had received the same treatment, were of the same age, species and quantities within each pot. In creating a generalised (species and age) model the influence of leaf area on reflectance spectra and the individual absorption features should be considered. Although we did not specifically measure LAI effects on our model, the inclusion of a REP variable in the ALL class model, could be used to evaluate variations in LAI values. Darvishzadeh et al. [2008b] showed that the REP, although not the best predictor for LAI in a heterogeneous grassland, shows a linear relationship with measured LAI values.

Unlike the waveband selection within dried material, the selection of wavebands we observed for the fresh material all included at least one waveband from within the VNIR of the spectrum. Baret et al. [1993] and Jacquemoud et al. [1992] in their works highlighted that the soil line and soil spectra are best measured in the VNIR region, as the relative reflectance indices or inter-band relationships created within this region are unaffected by moisture, and the soils composition, and through this the varying degrees of soil brightness, are clearly observed. Including a waveband from within this region in combination with wavebands from the SWIR region provides waveband combinations suitable for creating a soil adjusted vegetation indice. Similar soil indices such as the transformed soil adjusted vegetation index (TSAVI) or modified soil adjusted vegetation index (MSAVI) [Qi et al., 1994; Baret and Guyot, 1991] have been used to discriminate backgrounds

of different brightnesses created by reflectance of different soil types.

Wavelengths selected for fresh material, when applied to dried material, predict nitrogen. Why the converse does not apply is that measures of dried material are essentially free from the "noise" created by fresh material. Dried material is unaffected by soil background, leaf structure or water, therefore wavelengths that are strong protein or nitrogen predictors, but are influenced by "vegetation structure noise" are masked when measuring fresh plant material (e.g. the 2^{nd} overtone bonds), but can be selected by models created on dried material.

It might have been expected that different species of similar phenological stages would share wavebands within their selected models. Contrary to this our work suggests that it is important not to categorise plants into phenological stages, but rather different species be categorised according to their shared current physical structures.

2.4.2 Widened absorption feature models

Widening of absorption features increased the predictive power of models. A widened feature, would allow for variability of measurements made on multiple instruments with different calibrations and yet ensure that the biochemical absorption feature is still captured. Although we would expect neighbouring wavelengths to be more alike (multi-collinearity), if the averaged wavelengths include a reflectance value which is very different from its neighbours this will reduce its predictive power and it will no longer be amongst the selected wavelengths. The widening of an absorption feature makes sense when one considers that most investigators are using field and airborne instruments with differing calibration settings. Widening of an absorption feature would also potentially reduce the effects caused by increased noise associated with first derivative data transformations, and thereby also result in better predictive models. Mutanga and Skidmore [2004b]; Kokaly [2001]; Curran [1989] highlighted that at the centre of wavelengths features might saturate at relatively low levels, while widening a feature could act as a means to avoid this saturation. We have shown that the predictive power is not reduced by widening the features, but the influence of multi-collinearity of the widened features should be further investigated.

2.5 Conclusion

In respect to furthering our understanding towards prediction of nitrogen concentration *in-situ* our findings highlight that models created on fresh material should include wavebands from both the VNIR and SWIR regions of the spectrum, by doing so soil brightness effects can be integrated into the model. Widening of absorption features not only increases the predictive power of models, but it would allow comparisons between studies made with different spectroradiometric instruments having different waveband centres.

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Chapter 3

Plant age impacts, on forage-nutrient predictions derived from spectroradiometry*

*This chapter is based on the following paper: Knox, N.M., Skidmore, A.K., Schlerf, M., Groen, T., Prins, H.H.T., van Wieren, S.E., van Langevelde, F., de Boer, W.F., Heitkönig, I.M.A., Mwakiwa, E., Pretorius, Y., Grant, C.C., and Slotow, R. The influence of plant age, on predicting forage-nutrient concentrations derived from spectroradiometric data. In review, after resubmission, *International Journal of Applied Earth Observation and Geoinformation*.

Abstract

To study the seasonal fluctuation of nutrients within grasses using hyperspectral data, there is need to study the effect that takes place on spectra, not only with respect to nutrient variation, but also the additional variation created by changes in plant age (phenology). In this paper the integration of plant age in grasses, into models predicting nutrient concentrations from spectroradiometric data were studied. Two commonly applied empirical methods, partial least squares regression (PLSR) applied to a full spectrum and stepwise multiple linear regression (sMLR) applied to a reduced spectrum, were used on spectra collected from grass samples of variable ages. Grass samples were analysed for concentrations of forage-quality nutrients (nitrogen, phosphorus, and fibre). Regression models were applied, with and without, the addition of the co-variate plant age. Plant age, was shown to be important in the outcome of prediction models. A full spectrum PLSR model takes variability in plant age into account through having higher loadings in the regions of the spectrum associated with plant physiological development. For the three nutrients predicted by PLSR, without plant age, the R^2_{CV} values ranged between 0.59–0.81. With the addition of plant age R^2_{CV} values ranged between 0.62–0.82. sMLR using a reduced spectrum showed decreases in number of model variables required and/or an increase in R^2_{adj} values when the co-variate plant age was included R^2_{adj} 0.50–0.66 without and R^2_{adj} 0.48–0.78 with plant age. PLSR, when compared to sMLR, could predict nitrogen, fibre and phosphorus with higher R^2 (up to a 19% increase). Integration of plant age, either for interpretation (PLSR) or as a co-variate (sMLR), into regression models was shown to be an influential variable in creating nutrient fluctuation models.

3.1 Introduction

Being able to map continuous biophysical (chemistry and physical) plant variables allows nutrient fluxes, and system productivity to be investigated, and provides input into models analysing ecosystem processes. The possibility of creating such spatially explicit quantitative data has driven research in various biomes e.g. forests or woodland [Johnson and Billow, 1996; Curran et al., 1997; Smith et al., 2002; Huang et al., 2004; Ferw-

erda and Skidmore, 2007; Asner and Martin, 2008, 2009], agricultural land [Takahashi et al., 2000; Thenkabail et al., 2000; Monteiro et al., 2007] and grassland - both pasture and natural [Lamb et al., 2002; Mutanga et al., 2004b; Schut et al., 2005; Cho et al., 2007; Gianelle and Guastella, 2007; Darvishzadeh et al., 2008a].

In African savanna systems, many herbivores migrate large distances. These migrations have been linked to fluctuations in nutrients between seasons, in particular phosphorus and nitrogen levels [McNaughton, 1990; Prins, 1996]. Such seasonal nutrient fluctuations, and the extent of savannas observed in these ecosystems, lends itself to remote sensing applications. Use of remote sensing techniques, would allow for repeatable measurements, at reduced costs, compared to physical field measurements. An algorithm robust enough to monitor these natural systems, would not only have to detect seasonal fluctuations in nutrient levels, but would also need to account for phenological changes to plants.

Most studies into mapping of plant biochemical variables have been site-specific. Martin et al. [2008] investigated spatial variation of nutrients and applied nutrient algorithms developed for single sites to multiple study sites, with limited success. It would seem that currently there is insufficient understanding gathered within site-specific areas to allow extension of algorithms to multiple sites. Understanding of a single site would include the understanding of factors such as plant phenological cycles, and species variation in respect to changes in nutrient concentrations. As a plant develops, water content, cell structure and function will alter. These physiological alterations are evident in the reflectance spectrum [Kokaly et al., 2009; Kumar et al., 2001]. Changes in spectral absorption features would be associated with not only fluctuations in nutrient levels but also associated phenological information [Asner, 2004; Blackburn, 1998; Kokaly and Clark, 1999; Kokaly et al., 2009]. Linking the aging of plants to spectroscopic models of nutrient concentrations would potentially allow for seasonal monitoring of nutrients.

The aim of this paper is to show that prediction of nutrients, with spectroscopic data, should be integrally related to the inclusion of field knowledge, in this instance the variable plant age (phenology). Field knowledge is either required as a variable input into models or as an aid for the interpretation of model output. To reduce complexity, this study was conducted as a controlled greenhouse experiment. The plant nutrients to be predicted

were nutrients associated with the quality of grass forage. A full spectrum and reduced spectrum regression approach into modelling of the nutrient concentrations was applied[1]. The hypotheses tested were:

1. The full spectrum (PLSR) approach captures both plant age and nutrient information in the model variables (i.e. loadings) compared to a reduced spectrum approach (sMLR) that only uses wavelengths /absorption features linked to the specific nutrient in question. The PLSR models will produce models with higher R^2 values and lower root mean square error (RMSE) than sMLR models.

2. Through the addition of a plant age co-variate as an additional variable in PLSR and sMLR models, both approaches will have increased R^2 values and lower RMSE values.

3.2 Materials and methods

3.2.1 Greenhouse and samples

In a controlled greenhouse setting, two tropical grass species important for forage, *Digitaria eriantha* and *Urochloa mosambicensis* [van Oudtshoorn, 1992], were grown from seed. The two species were grown in separate pots on soils with three different nitrogen treatments (0.05, 0.125 and 0.2 % N per 1 kg soil). Pots were placed in a randomized layout. For the growth phases, conditions within the greenhouse were maintained at a constant temperature of 25°C, with 12 daylight hours and daily watering. Three weeks after seed germination, the number of germinated grasses within the pots were thinned. Sufficient grasses were left in each pot so as to ensure that the soil would be covered by vegetation at the time that spectra were measured.

Four plant age classes were differentiated in the analysis: seedling, adult, flowering and dormant. Ideally, samples of both species should have been used in each of these four stages, however the germination rates of *U. mosambicensis* were low and there were only sufficient numbers of germinated

[1] further background information on the regression approaches, as applied to spectroscopic data, are provided in appendix A

seed to be included in a single development stage. It was decided to analyse the *U. mosambicensis* samples as adults, because at this stage the plant material covered the soil. The description of the grass morphology in the different age classes is outlined below.

At seedling stage, the *D. eriantha* seedling canopy was morphologically a tufted, erect grass standing approximately 15–25 cm high. The adult stages of both *D. eriantha* and *U. mosambicensis* were without inflorescence's and reached a maximum height of 70 cm. *U. mosambicensis* formed denser tufts and their leaves were slightly broader than those of adult *D. eriantha* plants. Spectral measurements of the flowering stage were taken once a minimum of 2 inflorescences had fully opened. Because of a time lag in flowering under the different nutrient applications, the spectral measurements of the flowering stage were split and taken on two separate occasions, with one week between the measurements.

Following flowering, to invoke dormancy in the remaining samples, greenhouse conditions were adjusted. Samples were watered weekly and the temperature allowed to drop over night to a minimum of 10°C. Samples were considered dormant when all leaves had browned. Morphologically, the dormant grass tufts had opened and sagged. A direct spectral measurement of these samples would result in the inclusion of soil background within the spectra. To ensure that the soil was completely covered during spectral measurements, samples were bunched into tufts prior to taking a measurement. The number of samples analysed for each plant age class is presented in table 3.1.

3.2.2 Measurements

Spectral measurements

Spectra were measured using a GER 3700 spectroradiometer (Geophysical and Environmental Research Corp.). The GER 3700 was fitted with a 10° optic, placed on a tripod at a 15° viewing angle, 80 cm above the pot rim level, creating a field of view (FOV) of 14 cm in diameter (the diameter of the pot size at rim level was 19 cm). Mounting the spectrometer at this height, allowed for the projected plant growth between the seedling and flowering phase, and ensured that the same setup could be maintained

Table 3.1: Grass age classes, the time taken until spectral measurements could be made and numbers of samples included in each class

Code	Species	Age class	Weeks from sowing	Samples
DES	*D. eriantha*	Seedling	5	21
DEA	*D. eriantha*	Adult	8	38
UMA	*U. mosambicensis*	Adult	10	27
DEF_{nl**}	*D. eriantha*	Flowering	10	7
DEF	*D. eriantha*	Flowering	11	19*
DED	*D. eriantha*	Dormant	16	39

* These 19 samples were only included in calculations for Fibre see section 3.2.1; $_{nl**}$= samples that were treated with 0.05 % N per 1 kg soil

for all measurements. The calibration panel (Labsphere, Inc, Sutton, NH), used for converting radiance to absolute reflectance, was measured at a distance of 31 cm from the optic, creating a FOV of 5.5 cm in diameter. The calibration panel was only 225 cm^2, and thus a FOV of this size ensured an accurate reading of the panel. A halogen lamp was placed at nadir on the same level as the optic, illuminating the full field of view.

Potted plants were transferred from the greenhouse to the laboratory for spectral measurements. A pot was fixed in place (to ensure the FOV was located above the pot centre) for a group reading. One group reading consisted of a measure of the calibration panel and a set of 5 readings of the sample. In order to reduce directional effects, caused by leaf orientation within the canopy, the pot was rotated by 90°, and the next group reading taken [Mutanga et al., 2003; Cho and Skidmore, 2006]. The 20 spectral readings taken per pot were averaged to obtain a single spectral reading per sample.

Chemical analysis

After completing spectral measurements, grass samples were clipped 1 cm above the soil line, bagged and oven-dried at 70°C for 24 hours. During the oven drying process the *D. eriantha* flowering (DEF) samples (table 3.1) were mistakenly dried for part of the cycle at 105°C. Proteins denature at temperatures above 70°C, these 19 samples were therefore excluded from

analyses of nitrogen and phosphorus, but fibre concentrations were still analysed. Prior to chemical analysis, all oven-dried samples were ground through a 1 mm Wiley steel mill.

Nitrogen and phosphorus concentrations were determined using a modified Kjedahl procedure. Samples were initially digested in a mixture of sulphuric acid, selenium and salicylic acid [Novozamsky et al., 1983]. Following digestion, the samples were colorimetrically measured using a continuous flow analyser (SKALAR SAN plus). Fibre (Acid Detergent Fibre - ADF) concentrations were determined according to the ANKOM filter bag procedure, using an ANKOM $^{200/220}$ fibre analyser (ANKOM Technology, Macedon, NY, USA). The analysis procedure for ADF required 0.5 g of dried plant material. There was insufficient dried material to perform both the Kjedahl and ANKOM analysis procedures for nine seedling samples, thus only 142 of the total 151 samples have been analysed for their fibre concentrations. All nutrient concentrations are presented as percentage dry matter.

3.2.3 Data Analysis

All statistical analyses was performed using the statistical software "R" ver. 2.6.2 [R Development Core Team, 2008].

Pre-processing

All data (reflectance and nutrient) were first mean centred prior to applying the different regression approaches. Mean centering allows for comparison between the effects of different wavelengths on variable loadings produced in the PLSR models [Geladi and Kowalski, 1986]. Mean centering is not a standard pre-processing technique for sMLR, but allows for direct comparison with the PLSR output, because all data were treated uniformly. Prior to implementing the sMLR tests for each nutrient, modles were first performed using both the reflectance and then mean-centred data, to determine if the transformation altered model outcomes. It was verified that applying mean-centering did not alter the outcome of the sMLR algorithms, and therefore to allow for direct comparison with PLSR models the mean-centred data were used in the sMLR.

Stepwise regression

Spectrum reduction Numerous methods have been developed for reducing a hyperspectral data into a few key variables that can be used as input for sMLR (see appendix A). Except for selection of only wavelengths that have been linked to physical bond vibrations of a nutrient of interest, other reduction methods also select and include other parts of the spectrum that are linked to the particular dataset in question. Reducing a spectrum to include spectral areas that link to both plant physiology and nutrient concentrations will result in better fitting models specific for a test dataset, but makes models difficult to transfer to other datasets. Thus in trying to create models that can predict nutrients concentrations irrespective of plant age, it was decided that the method of reduction should only contain spectral features associated with the nutrient of interest. With this method it would be possible to see how much information is obtained using only these parts of the spectrum, before additional information about the plants development is added as a co-variate to modelling. The wavelengths selected are features that have been identified by multiple authors [Card et al., 1988; Peterson et al., 1988; Curran, 1989; Johnson et al., 1994; Fourty et al., 1996; Martin and Aber, 1997; Kokaly and Clark, 1999; Kumar et al., 2001; Soukupova et al., 2002; Mutanga, 2004; Ferwerda, 2005; Cho and Skidmore, 2006]. The different wavelengths used in this study for the different nutrients is given in table 3.2.

To test the two hypothesis stated in the introduction, the following points were considered in creating the input libraries for the sMLR analysis:

1. If plant age plays no role in predicting nutrient concentration levels, then an sMLR approach that uses only wavelengths associated with a particular nutrient should yield a similar prediction output (adjusted R^2 and RMSE) to a full spectrum (PLSR) approach. The wavelengths with maximum loadings of different wavelengths in a PLSR model should correspond to those variables associated with a particular nutrient.

   The reduced spectral library, containing only the wavelengths associated with the nutrient of interest, were used to compute the stepwise process outlined below.

2. Plant age (PA) is added as an additional variable (categorical) to-

Table 3.2: The absorption features used as input for the stepwise regression (see section 3.2.3) calculations[a]

Nutrient	Absorption Features (nm)
Nitrogen	430*, 460*, 640*, 660*, 910*, 1020*, 1420*, 1510*, 1520, 1690*, 1730*, 1940*, 1950*, 1960*, 1980*, 2060*, 2130*, 2180*, 2200, 2240*, 2270*, 2290, 2300*, 2350*, REPg[b], REPc[b], REPd[b]
Phosphorus	990*, 1450*, 1490*, 1530*, 1540*, 1560, 1580*, 1720, 1750, 1780*, 1900*, 1910, 1950*, 1960*, 2000*, 2080*, 2100*, 2110, 2140, 2250*, 2270*, 2280*, 2310, 2320*, 2340*
Fibre - Cellulose	1410, 1470, 1490*, 1540*, 1550, 1730*, 1736*, 1770, 1780*, 1820*, 1920, 1924*, 1940*, 1950*, 2020, 2090, 2100*, 2260, 2270*, 2280*, 2300*, 2340*, 2350*, 2380

[a] absorption features compiled from Card et al. [1988]; Peterson et al. [1988]; Curran [1989]; Johnson et al. [1994]; Fourty et al. [1996]; Martin and Aber [1997]; Kokaly and Clark [1999]; Kumar et al. [2001]; Soukupova et al. [2002]; Mutanga [2004]; Ferwerda [2005]; Cho and Skidmore [2006]

* absorption features associated with physical bond vibrations

[b] REP, calculated using a standard derivative (REPd), linear four-point interpolation (REPg) and linear extrapolation (REPc), formulae for the calculation of these different REP's are given in Cho and Skidmore [2006]

gether with the reduced spectral library as input in the sMLR procedure. If PA has no effect on the prediction of nutrients then the outcome of the sMLR models shoud be no different. By differences, we refer to the variables selected in the sMLR process and the prediction outcomes of the models. Using an Akaikes information criteria (AIC), the sMLR models with (PA) and without (nPA) the plant age variable were compared to determine the most parsimonious models [Crawley, 2006].

Both input data libraries outlined above had the following modified sMLR procedure applied:

Selection of variables in sMLR is sensitive to outliers and samples of high

leverage [Crawley, 2006]. To account for this, an iterative approach for selecting variables was developed. For each iteration, 75% were randomly selected and used to train a model. The model was trained using stepwise regression. Variables (absorption features) selected at the end of a training run were recorded.

For the first nutrient tested (nitrogen) it was determined at which point the same variables were consistently selected in 80% of the training models. These variables were considered to be features that would best describe variations in nutrient concentrations irrespective of phenological state. Starting from 50 iterations, in increments of 50, the number of iterations was increased until the stable point was reached. The stable point in this study was found to be 250 iterations, this value was then implemented for all remaining runs for all nutrients.

Following the 250 iterations, the selected absorption features, i.e. those variables selected in 80% of all training models, were used as variables to create a model on the entire dataset. The selected absorption features were applied to the full dataset, and the adjusted R^2 (R^2_{adj}) and RMSE are reported.

Partial Least Squares Regression

Prior to applying PLSR, the spectra were visually assessed for noise. Bands below 400 nm and between 1890–1910 nm were consistently noisy and thus removed.

Similar to the sMLR procedure outlined above, PLSR was run twice. Regressions were run firstly using only the spectral data cube, and then again with plant age added as a variable (converted to a numerical data type) to the independent data cube. The analyses were performed using the "pls" package [Wehrens and Mevik, 2007] within the statistical program "R". On the basis of a study by Mevik and Cederkvist [2004], we selected to run PLSR using leave-one-out cross validation (LOO). The number of latent variables (NLV) selected to model nutrient concentration was made by identifying the minimum prediction residual error sum of squares (PRESS) value [Geladi and Kowalski, 1986]. The outcomes of the PLSR models are described by the NLV selected, calculation of the R^2 for cross validation (R^2_{CV}) and root mean square error of prediction (RMSEP). Both the R^2_{CV}

Table 3.3: Basic statistics of the nutrient concentrations analysed

Nutrient	Mean (%)	Range (%)	Samples
Nitrogen	3.8	2.3–5.0	131
phosphorus	0.3	0.2–0.6	131
Fibre	27.7	21.3–32.6	142

and RMSEP values were calculated considering the NLV's used to describe a model.

The models that provided the highest R^2_{CV} and lowest PRESS values, without the plant age variable added for each nutrient, are graphically represented in the results. Rather than presenting each loading vector separately, the vectors are combined additively for the NLV used in the models. The graphical outputs are used in conjunction with the known absorption features related to physical properties of the nutrients (features marked with an * in table 3.2) to discuss the implications of the PLSR models.

3.3 Results

Across the spectral range numerous plant physiological features were visually pronounced in spectra taken of grases in different development stages (figure 3.1). Reflectance within the green region (± 550 nm), the red absorption and red-edge feature (650 nm, 670–720 nm), the near-infra red plateau, depth of water features (particularly at 1450, 1940, 1950 nm), and the ligno-cellulose absorption feature at 2100 nm, all showed the greatest spectral variations between the different age classes. Brightness differences on the NIR plateau, appears to be most characteristic difference between spectra taken of adult and flowering plants.

The statistics of the different nutrient concentrations measured in the chemical analysis are given in table 3.3. In figure 3.2, the concentrations of the forage nutrients is given for each age class. For each nutrient, the differences between the flowering and dormant classes were non-significant.

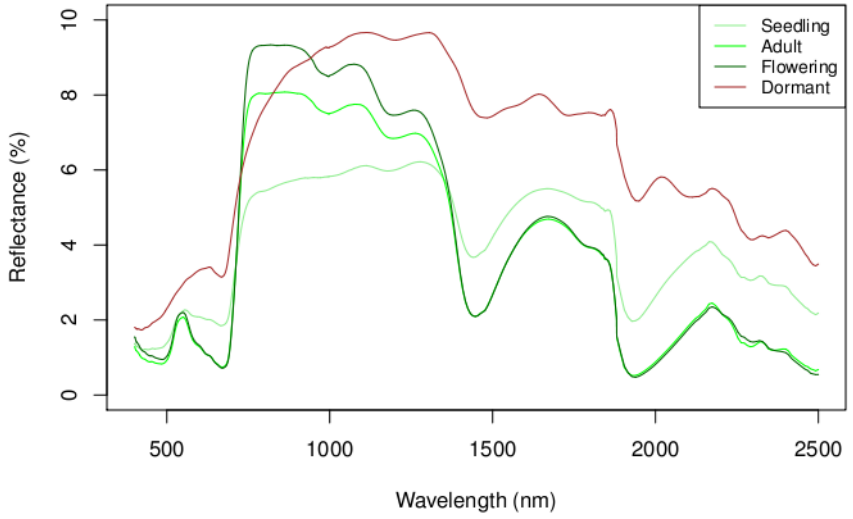


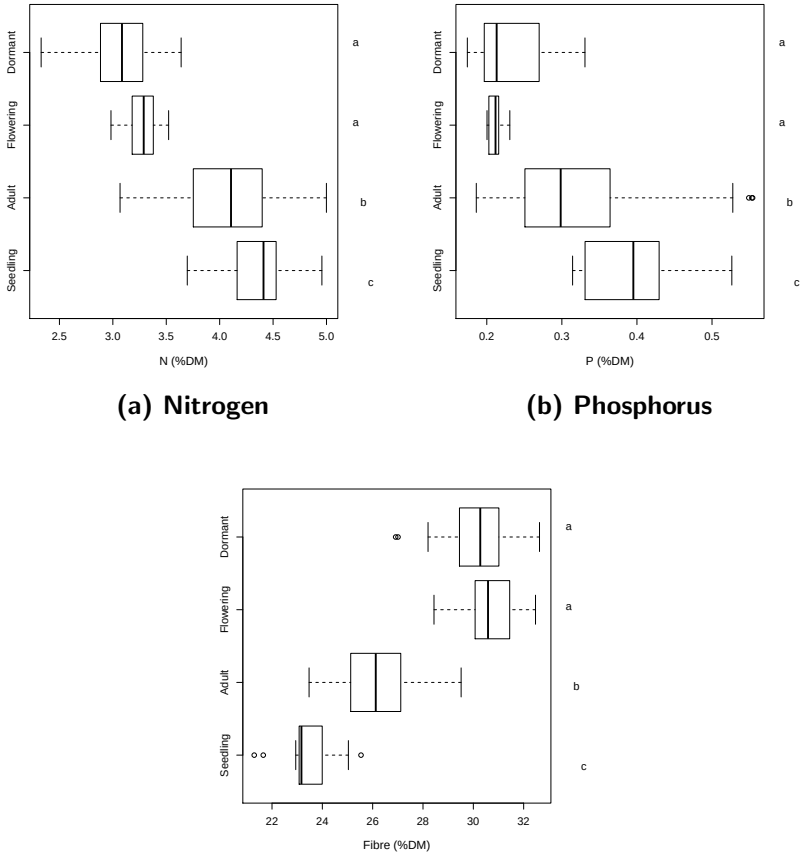
Figure 3.1: The average spectrum per age class. Reflectance values of the flowering and dormant spectra were adjusted down by a factor of 1.2, to compensate for brighter measurements resulting from the measurement set-up. Adjusting of spectra allow for an easier comparison of absorption features between the spectra of different age classes.

3.3.1 Regression with only spectral variables:

Reduced spectrum sMLR models using only spectral features were able to explain between 50% and 66% of the variation in nutrient concentration levels (table 3.4). The spectral features selected in the sMLR models were, for nitrogen and phosphorus, mostly associated with wavelengths that have been linked to bond vibrations (marked with an * in table 3.5). Only one of the fibre features was associated with a bond vibration (table 3.5).

Full spectrum PLSR models were able to explain between 59% and 81% of both the plant ages and nutrient variations in the output models (table 3.4). For all nutrients studied here, PLSR models when compared to the reduced spectrum sMLR models had higher R^2 values and lower root mean square error (RMSE) (table 3.4, nPA columns).

Figure 3.3 displays the sum of latent variable loadings used in each of the nutrient PLSR models. A grass spectrum is overlain in each of these figures to visualise where loadings occur relative to spectral features of a plant.



(a) Nitrogen **(b) Phosphorus**

(c) Fibre

Figure 3.2: The concentrations of forage nutrients for each age group measured. The letters to the right of the plot are the outcome of a Mann-Whitney U test to determine whether nutrients differed statistically (95%) between the different age classes. Different letters indicate a statistical difference.

Table 3.4: A comparison of the R^2 and RMSEP values obtained for the sMLR and PLS regressions, with (PA) and without (nPA) the addition of the variable plant age. The number of variables required in the respective models both with and without the variable plant age is presented in the last column.

Nutrient	Method	R^2 (nPA)	RMSEP (nPA)	R^2 (PA)	RMSEP (PA)	Variables (nPA, PA)
Nitrogen	sMLR	0.63	0.39	0.70	0.35	5,7
	PLSR	0.79	0.29	0.79	0.29	12,12
Phosphorus	sMLR	0.50	0.07	0.48	0.07	7,6
	PLSR	0.59	0.06	0.62	0.06	8,8
Fibre	sMLR	0.66	1.62	0.78	1.30	5,6
	PLSR	0.81	1.20	0.82	1.17	11,11

For the PLSR models the number of variables presented are the number of latent variables selected at the minimum PRESS value (see section: 3.2.3).

Table 3.5: Wavelength selection in the sMLR with (PA) and without (nPA) the addition of variable plant age. The variables marked with an * are features associated with physical bond vibrations.

Nutrient	Method	Selected absorption features (nm)
Nitrogen	nPA	430*, 1940*, 1960*, 2350*
Nitrogen	PA[a]	2060*, 2350*, age
Phosphorus	nPA[a]	990*, 1450*, 1540*, 1720, 2250*, 2280*
Phosphorus	PA	2250*, age
Fibre (C)	nPA	1470, 1550, 2270*, 2340*
Fibre (C)	PA[a]	1550, age

Using the Akaikes information criteria (AIC), sMLR models were compared for each of the forage nutrients. The models marked with [a] had the lowest AIC values and are considered superior.

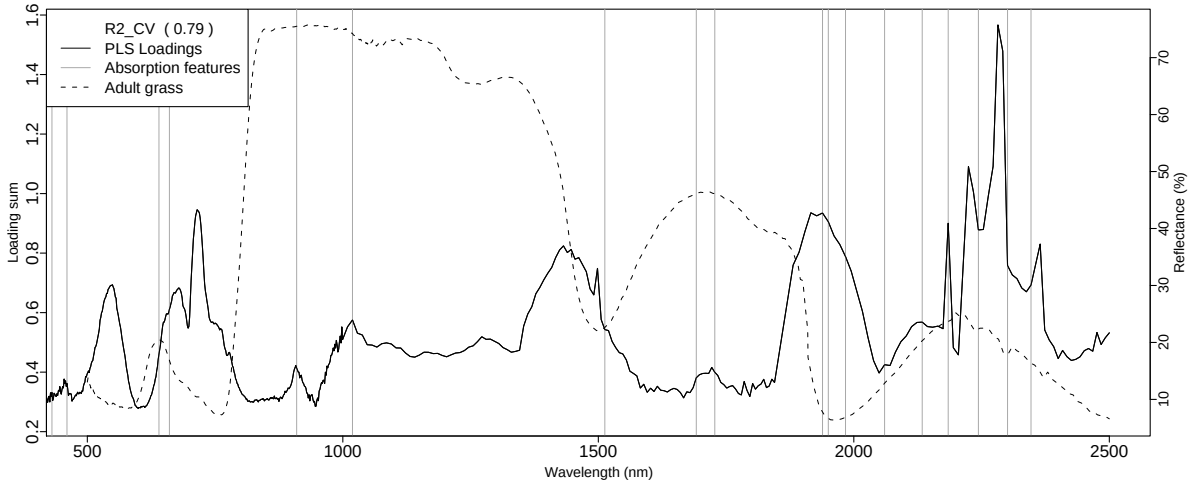
Absorption features linked to bond vibrations (table 3.2 -marked with *) of the associated nutrient are overlain on the figures to highlight where the maximum loadings occur with respect to these features.

3.3.2 Regression with spectral and plant age variables:

It was hypothesized that with the inclusion of the variable plant age into the PLSR and sMLR model, the predictive capabilities of both approaches would improve (i.e. increased R^2 and decreased RMSE values) and that these values would be similar for either approach.

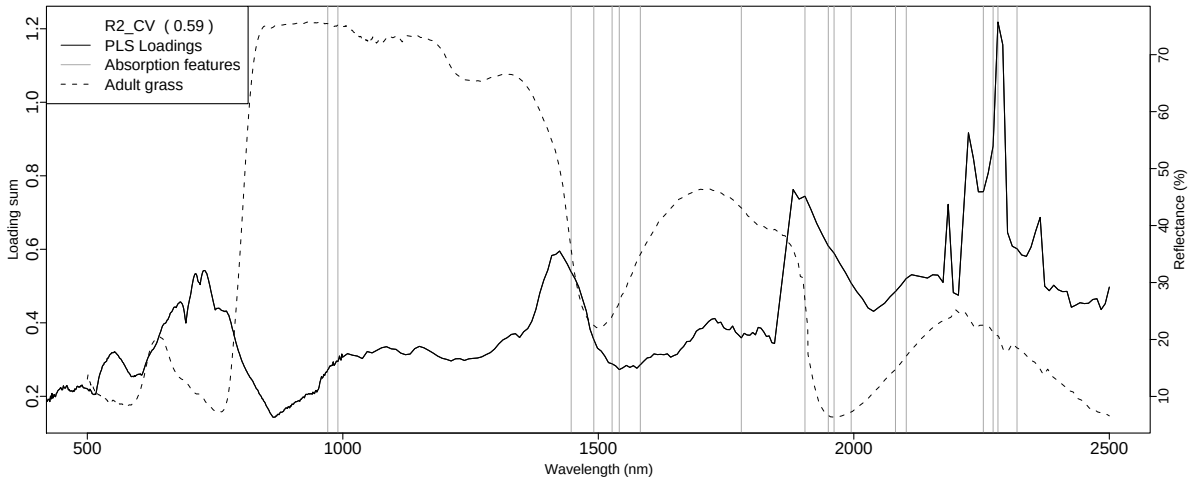
The number of variables needed to model the nutrient concentrations, was reduced (table 3.5). The predictive capabilities (lower AIC and higher R^2) or complexity (reduced numer of variables) of sMLR models improved for all nutrients. The features selected by sMLR models for all nutrients included the plant age variable. Most of the variables that were selected in these models had also been selected in the modelling performed without the variable plant age (table 3.5).

Similar to the sMLR models, plant age was a variable with a high loading weight in the PLSR models. Unlike sMLR the addition of plant age to PLSR models only provided marginal improvements to the various models capabilities (table 3.4 - PA columns vs nPA columns). In the PLSR models there were no notable differences in the number of latent variables required to model the respective nutrients (table 3.4 - Variables column). This indicates that plant age was already accounted for in the full spectrum models and by including it as a variable no further improvements, to the modelling procedure, were made.



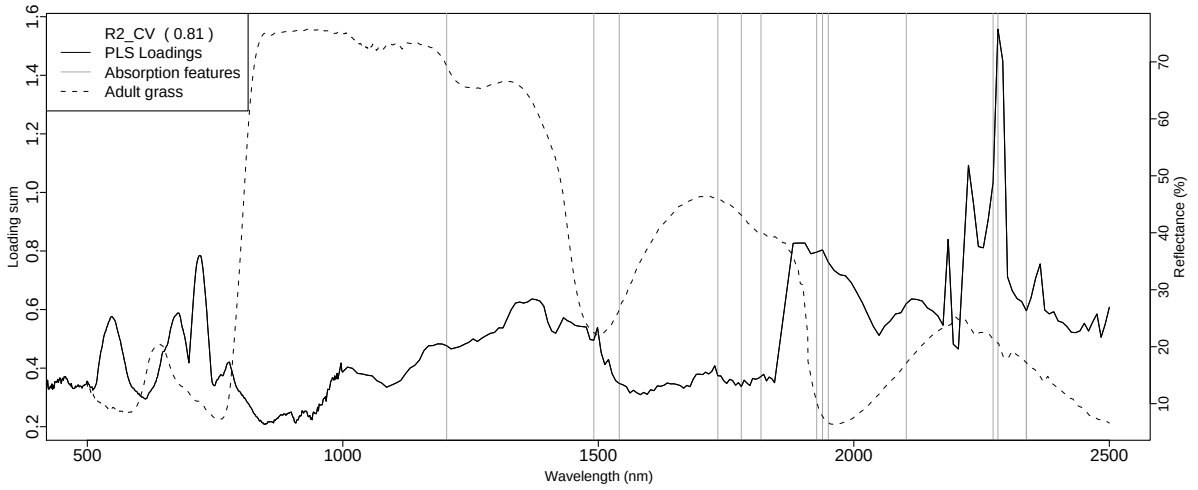
(a) Nitrogen

Figure 3.3: Part 1 of 3: a) PLS loading model for nitrogen, for the detailed figure explanation please see the later description...



(b) Phosphorus

Figure 3.3: Part 2 of 3: b) PLS loading model for phosphorus , for the detailed figure explanation please see the later description...



(c) Fibre

Figure 3.3: Part 3 of 3: c) PLS loading model for fibre.
The PLSR models with the highest cross validation accuracy (R^2_{CV}) for each nutrient analysed. A grass spectrum from the adult class is overlain to see which regions in the vegetation spectrum result in the highest loading scores. The loading scores displayed in each figure is a sum of the loading weights for all the NLV selected to describe the model. Loading values for a latent variable might be negative of positive, all values were made positive prior to being summed.

3.4 Discussion

In this study, full and reduced spectrum regression models were compared for the prediction of forage quality nutrient concentrations in plants of different ages. Partial least squares regression (PLSR) was found to be a method that could predict the concentrations of nitrogen, fibre, and less reliably phosphorus, in tropical grasses, irrespective of the age of the grass.

Examination of the PLSR model variables, through plotting the sum of loadings for each nutrient (figure 3.3), allowed for a visual interpretation of why a stepwise multiple linear regression (sMLR) approach, using only known absorption features, would be unsuccessful in predicting nutrient concentrations. The highest spectral loading values, for each individual nutrient, did not coincide with only the absorption features associated with the particular nutrient of interest. Spectral features, such as the red-edge region (670–780 nm), and the far shoulder regions (of both the near and shortwave-infrared peaks) in the 1000–2000 nm range, had high loadings. These regions have been associated with changes in plant physiological state, including pigments and water absorption features [Curran, 1989; Elvidge, 1990; Fourty et al., 1996; Blackburn, 1998; Kokaly and Clark, 1999], and concurred with the spectra taken of the different age classes (figure 3.1). The highest loading values for each of the nutrients occurred at the wavelength 2280 nm. This wavelength has been associated with a $C-H$ stretch/CH_2 deformation, and linked to concentrations in starch, cellulose [Curran, 1989], sugar [Fourty et al., 1996] and lignin [Martin and Aber, 1997]. To capture the variation in both plant age and nutrients a greater component of the spectrum is required, or information associated with a plants physiological state is necessary.

In a field situation, or when upscaling to imagery, there are most likely multiple phenological states and species. Multiple species have, however, been shown to have unique spectral signatures [Schmidt and Skidmore, 2001; Mutanga et al., 2004b; Vaiphasa et al., 2007; Asner and Martin, 2009]. Mutanga et al. [2004b] showed that tropical grass species and sodium interacted to change spectral reflectance across most of the spectrum, particularly so in the visible part. Asner and Martin [2009] suggested an approach for integrating chemical, spectral and species fingerprints. Our findings support this notion that both plant physiological characteristics and chemical characteristics should be combined and considered within the spectroscopic

analysis.

In conclusion the development of models for predicting nutrients, a PLSR approach captures and includes more information, in the output latent variables, than just the dependent (nutrient concetration) dataset. A reduced spectrum sMLR model is unable to do so directly, but improves when ancillary data were added (this might also be additional wavelengths associated with ancillary data). If these results are extended to a field situation, it would be expected that a simpler sMLR model which includes ancillary data could easily be transferred between sites. A PLSR model, by comparison would contain additional information in the model output that is site specific. In this study the ancillary variable added was plant age, but in a field situation these data would likely also include variables such as species information, soil characteristics, or terrain data.

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Chapter 4

A comparison of spectroscopic phenological algorithms, for differentiation of plant age in savanna grasses*

*This chapter is based on the following paper: Knox, N.M., Skidmore, A.K., van der Werff, H.M.A., Groen, T.A., de Boer, W.F., Prins, H.H.T., Kohi, E., Peel, M. A comparison of spectroscopic phenological algorithms for the differentiation of plant age in savanna grasses. In review, *International Journal of Remote Sensing.*

Abstract

Being able to classify a plant according to its phenological stage (including transitions between age classes), allows for examination of micro-topographical effects on plant growth, improvement on the accuracy of species discrimination, and will improve our understanding of temporal variations in plant phenology. In this paper five phenological algorithms (including a newly proposed PhIX algorithm) were analysed for their ability to statistically differentiate grasses of different ages, in the sequenece of their ages. Spectra of grasses of different ages were collected from grasses grown in a greenhouse study. These spectra were used to determine if NDVI, NDWI, CAI, tied SWIR2, and the newly proposed PhIX algorithm could sequentially discriminate grasses of different ages. The PhIX algorithm was defined as:

$$\frac{A^n_{VNIR} + \log(A^n_{SWIR2})}{A^n_{VNIR} - \log(A^n_{SWIR2}) + 1}$$

where A^n_{VNIR} and A^n_{SWIR2} are the respective normalised areas under the continuum removed reflectance curve within the VNIR (500–800 nm) and SWIR2 (2000–2210 nm) regions. Both CAI and PhIX sequentially differentiated plant ages in the correct chronological order, while NDVI and NDWI could differentiate most age classes, but the plant age order was not chronological. The tied SWIR2 method could not differentiate classes, but a visual assessment showed that photosynthetic and non-photosynthetic material could be differentiated. CAI and PhIX were applied to a field dataset to see if defined phenological classes could be discriminated on mixed grass species collected as paired dataset over two consecutive seasons. Both algorithms performed well, showing an advance in phenology between the seasons. This work showed that phenological classes (in grasses) could be defined using either the CAI or PhIX algorithms, and applied to new datasets to classify the stage of phenological development.

4.1 Introduction

The response of an ecosystem to climatic variation is reflected in the growth response of vegetation. In order to understand the effects of human induced climate change on ecosystems, there has been an increased interest into means to evaluate vegetation phenology [Archibald and Scholes, 2007].

Remote sensing has been used to investigate phenology at various scales, from ecosystem [Asner et al., 2000; Asner and Heidebrecht, 2002; Archibald and Scholes, 2007; Dennison and Roberts, 2003; Elmore et al., 2005; Garcia and Ustin, 2001], through to regional, and continental scales [Beck et al., 2007; Bradley and Mustard, 2005; Bradley et al., 2007; Kathuroju et al., 2007; Marsett et al., 2006; Reed et al., 1994; Zhang et al., 2003].

Phenological studies, that have applied remote sensing technologies, have typically been approached in two ways:

1. An area is repeatedly studied to gain an idea of the temporal fluctuations in vegetation phenology. To observe phenological changes requires data of high temporal resolution, and consequently such studies have favoured the use of AVHRR and more recently MODIS data. The spectral range available in these data have resulted in most studies applying either normalised difference vegetation index (NDVI; Tucker [1979]) [Archibald and Scholes, 2007; Beck et al., 2008; Bradley et al., 2007; Reed et al., 1994; Zhang et al., 2003], or a combination of NDVI and the normalised difference water index (NDWI; Gao [1996]) [Delbart et al., 2005, 2006; Huesca et al., 2009; Koltunov et al., 2009; Peckham et al., 2008]. The output of these studies have been used to understand land cover changes [Bradley and Mustard, 2005], biomass estimates [Butterfield and Malmström, 2009] and climate changes [Cleland et al., 2007; Pettorelli et al., 2005].

2. The second approach to phenological studies, is to use the different stages of phenologic development in order to differentiate cover in terms of vegetation that is photosynthetic (PV) and non-photosynthetic (NPV) and the soil layer. The need to discriminate vegetation from soil background is of particular importance in grassland and savanna systems where the presence of bare soil patches confound vegetation remote sensing studies. The demand for this information has resulted in the development of the cellulose absorption index (CAI; Nagler et al. [2003]), as well as the tied SWIR2 method [Asner and Lobell, 2000]. The output from these studies have then been further applied to fire risk mapping, species identification, and crop modelling [Elmore et al., 2005; Garcia and Ustin, 2001; Huang and Geiger, 2008; Nagler et al., 2003]

Many of the studies that were conducted in arid, semi-arid ecosystems

have indicated that the phenological responses of grasses differ from trees, and are often problematic to evaluate [Archibald and Scholes, 2007; Butterfield and Malmström, 2009; Dennison and Roberts, 2003; Garcia and Ustin, 2001]. The difficulties have been attributed to the combination of both photosynthetic and non-photosynthetic grasses often present at the same time [Dennison and Roberts, 2003; Garcia and Ustin, 2001]. Grasses are water limited and rely on soil moisture for the onset of greening [Zhang et al., 2003], they tend to green later than trees and their greening response is masked by tree reflectance and is difficult to detect [Archibald and Scholes, 2007]. Because of the reliance of grass on rainfall events, grass phenological developments in drier environments are unpredictable, and might also include multiple growth responses over a season [Reed et al., 1994; Zhang et al., 2003].

Identification of grass phenological stages has been used for the evaluation of fire fuel conditions [Elmore et al., 2005], invasive species mapping [Bradley and Mustard, 2005; Huang and Geiger, 2008], and land cover classification [Asner et al., 2005; Garcia and Ustin, 2001]. Mingo and Oesterheld [2009] highlighted the selectivity of foraging herbivores to avoid senescent material. While estimating changes in grass biomass, Butterfield and Malmström [2009] and Marsett et al. [2006] highlighted how different phenological stages confound predictions. Bradley and Mustard [2005] and Huang and Geiger [2008] demonstrated that inclusion of grass phenological stages, increased the accuracy of mapping grass cover. An accurate and robust algorithm that can be used to readily identify the phenological stage of grasses would provide a useful tool to analyse such problems as these.

Considering the earlier findings of Asner et al. [2000]; Asner and Heidebrecht [2002]; Elvidge [1990]; Elvidge and Portigal [1990]; Nagler et al. [2000] both the visible near infrared (400–1400 nm) (VNIR) and shortwave infrared 2 (2000–2300 nm) (SWIR2) regions are considered to be the most relevant regions to analyse phenological information. Combining information from these two regions was felt would produce a useful means to identify phenological changes, in particular those associated with entering dormancy. The VNIR region would capture the changes in plant pigments and the SWIR2 region the development of cellulose and lignin as a plant ages [Elvidge, 1990]. In this paper a new phenological algorithm, using information combined from both the VNIR and SWIR2 regions, is proposed and compared with the four previously proposed algorithms listed above.

If a phenological algorithm is applied either in continuous monitoring or at individual points in time, it is necessary to be able to interpret the output value generated from the application. For example, if analysing two pixel values of 0.23 and 0.54 produced after applying an algorithm to an image, it is necessary to be able to interpret these values. If performing a spatial, point in time analysis the production of phenological age classes would aid interpretation of these values, in a temporal analysis a division of age classes is needed and these classes should be sequential in terms of plant development, e.g. seedling → adult → senescent.

The aim of this paper is to evaluate phenological algorithms in terms of robustness and broad applicability, for both point in time and temporal studies. The algorithms were compared firstly for their ability to statistically differentiate between different plant development stages, and secondly whether the separation of classes was chronological in terms of plant development.

4.2 Experimental design and datasets

The newly proposed algorithm was developed using a dataset obtained from a greenhouse experiment (4.2.2), this dataset was also used to test four other phenological methods already in use, including the normalised difference vegetation index (NDVI) [Tucker, 1979], normalised difference water index (NDWI) [Gao, 1996], cellulose absorption index (CAI) [Nagler et al., 2000], and the tied SWIR2 method [Asner and Lobell, 2000]. The respective algorithms were assessed to determine if they could separate the phenological classes sequentially. If this was fulfilled, phenological classes were created from this dataset. The classes were then applied to a field paired-dataset collected in a mopane-grassland savanna in two consecutive seasons. This allowed for an evaluation into how the algorithms performed in a diverse (topographically and in terms of plant species) field environment. The algorithms are described in section 4.2.1. The greenhouse and field datasets, and method of spectral collection, on which the algorithms were tested, are described in sections 3.2.3 and 4.2.3.

4.2.1 Algorithm development and evaluation

The PhIX algorithm

In the newly proposed PhIX algorithm information, from the VNIR and SWIR2 regions are combined to create a new phenological algorithm. Two separate continua were created over the VNIR and SWIR2 regions. The start and end points of the continua were fixed. The VNIR continuum stretched between 500–800 nm. By starting at 500 nm noise associated with atmosphere, in the blue region was removed, but the green and red regions associated with plant pigments remain. The endpoint of 800 nm was selected as a point where all phenological stages reached the NIR plateau. The SWIR2 continuum stretched between 2000–2210 nm, the start point was defined by the end of the water absorption feature located at 1950 nm [Curran, 1989; Fourty et al., 1996], and the end point by the end of the cellulose absorption feature [Elvidge, 1990] observed in dormant grasses. In figure 4.1 the average continuum removed spectra are shown to highlight the observed differences seen between grasses of differing development stages.

Band centre, band depth, feature width, and symmetry have all been generated from continuum removed spectra to describe absorption features, in both geological [van der Meer et al., 2001] and more recently vegetation applications [Chen et al., 2007; Huang et al., 2004; Kokaly and Clark, 1999; Kokaly, 2001; Mutanga and Skidmore, 2004a; Schmidt and Skidmore, 2003]. These feature variables were found to be unsuitable in describing the variation in phenological classes, and thus a new variable for describing the continua was used. It was found that the area under the reversed continuum could statistically differentiate age classes (figure 4.2). Statistical separation of classes was tested by performing a Tukey HSD test [Crawley, 2006]. The area variable was normalised (through maximum value normalisation) to allow for comparison between the separation of the VNIR and SWIR2 regions.

Although the normalised VNIR areas differed significantly between classes (figure 4.2a), it did not do so in the order of phenological development. In the SWIR2 region especially the dormant class was significantly different from all the other classes (figure 4.2b). To linearize the difference in these SWIR2 classes, the normalised SWIR2 values were logged. Combining the VNIR and the SWIR2 properties, we developed a new index to separate

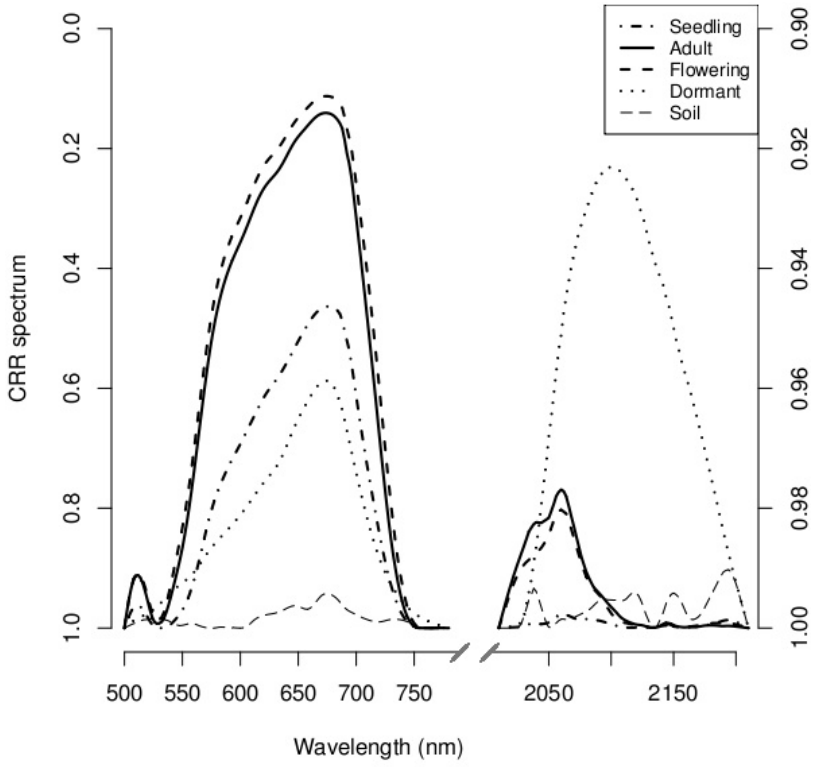
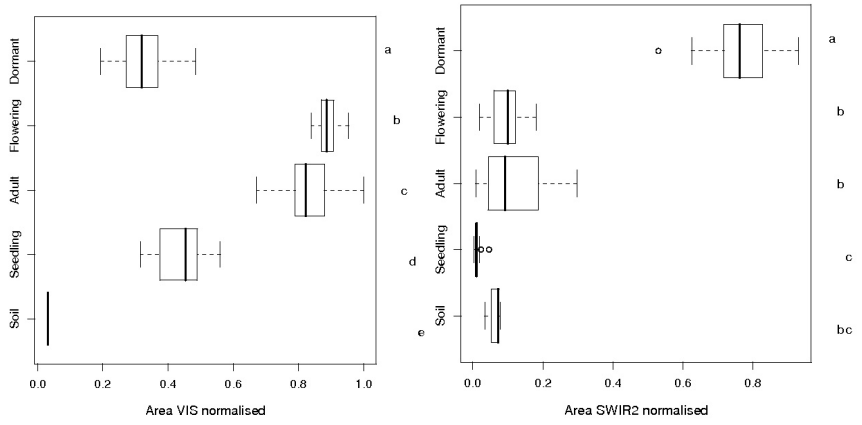


Figure 4.1: The average CRR spectrum, for each age class grown in the greenhouse experiment, in the VNIR and SWIR2 region of the spectrum. Because the PhIX algorithm is calculated using the area under the CRR curves, the curves have been inverted to allow for an easier visual assessment of the areas under each curve. Note: the scales for the VNIR and SWIR2 region differ.

the classes in sequence of phenological development:

$$PhIX = \frac{A^n_{VNIR} + \log(A^n_{SWIR2})}{A^n_{VNIR} - \log(A^n_{SWIR2}) + 1} \tag{4.1}$$

where A^n_{VNIR} is the normalised area under the VNIR continuum curve and A^n_{SWIR2} is the normalised area under the SWIR2 curve.



(a) Area VNIR **(b) Area SWIR2**

Figure 4.2: The statistical (Tukey HSD) separation (95% CI) of the different age classes of samples, grown in the greenhouse experiment, using the normalised area under the CRR curve: a) is the area under the VNIR curve, and b) is the area under the SWIR2 curve. A different letter on the right margin indicates that an age class differs significantly.

Phenological algorithms for comparison

A number of phenological algorithms are already in use. The potential of these algorithms were evaluated and the outcomes compared with the newly proposed algorithm, using the evaluation method described in section 4.2.1. These algorithms were: NDVI (Eq. 4.2), NDWI (Eq. 4.3), CAI (Eq. 4.4), and the tied SWIR2 (Eq. 4.5). Only the tied SWIR2 algorithm utilises hyperspectral images.

$$NDVI = \frac{R_{NIR(830)} - R_{Red(680)}}{R_{NIR(830)} + R_{Red(680)}} \tag{4.2}$$

where $R_{NIR(830)}$ is reflectance at 830 nm in the NIR region, and $R_{Red(680)}$ is reflectance at 680 nm in the red region.

$$NDWI = \frac{R_{NIR(860)} - R_{SWIR(1240)}}{R_{NIR(860)} + R_{SWIR(1240)}} \tag{4.3}$$

where $R_{NIR(860)}$ is the reflectance at 860 nm in the NIR, and $R_{SWIR(1240)}$ is the reflectance at 1240 nm in the SWIR region.

$$CAI = 0.5(R_{2000} + R_{2200}) - R_{2100} \tag{4.4}$$

where $R_{2000}, R_{2100}, R_{2200}$ are the reflectances at 2000 nm, 2100 nm and 2200 nm respectively.

$$SWIR2_{tie} = \begin{bmatrix} R_{2000} \\ \vdots \\ R_{2300} \end{bmatrix} - R_{2030} \tag{4.5}$$

The tied SWIR2 method normalises, through subtraction, all reflectance values in the range of 2000–2300 nm to the reflectance value at 2030 nm. Unlike the other methods presented, the tied SWIR2 algorithm does not produce a single output value, but rather a normalised spectrum. The normalised spectrum can then be applied as endmembers for further phenological analysis.

Algorithm evaluation

Each algorithm was applied to a greenhouse dataset of which the ages of the samples was known. Using a Tukey HSD test [Crawley, 2006] it was tested if the algorithms were capable of stastically differentiating the age classes. This analysis was used to evaluate the algorithms for their potential to ascertain the spatial heterogeneity of phenological classes at a single point in time. To evaluate the algorithms for their potential in temporal studies the different classes generated in the Tukey HSD test were analysed to determine if the separation of classes was sequential, e.g. seedling → adult → senescent.

If an algorithm was able to sequentially separate out classes, classes per age category were then defined for this algorithm, using the greenhouse dataset. A class was defined as the data falling within the inter-quartile range of each age category. If classes followed a chronosequence, but were not significantly different, the classes were combined to form a single class. Combining classes was done by creating the broadest range between the respective classes inter-quartile ranges (e.g. a combined range could be

composed of the lowest value of one class and the highest value of the other second class). The algorithm and these classes were then applied to a field dataset. In interpreting the outcome of the algorithm from the field dataset, values between two defined class were classified as Transition, values above the Dormant class range were classified as Senescent, and values below the lowest range were classified as Unclassified.

If a phenological algorithm is to be broadly applied it should also be able to differentiate between vegetation (in any stage) and soil. Bare soil spectra were also included and classified in the algorithm evaluation to determine if this background could be discriminated.

4.2.2 Datasets

Greenhouse dataset

Two tropical grass species, *Digitaria eriantha* and *Urochloa mosambicensis*, were grown in pots from seed, and were placed in a randomized layout. Grasses were grown under three different nitrogen applications (0.05, 0.125 and 0.2 % N per 1 kg soil). Conditions in the greenhouse during the growth phases, were maintained at a constant temperature of 25°C, with 12 daylight hours and daily watering.

Urochloa mosambicensis had low germination rates, and there were only sufficient numbers of germinated seed to be included in a single growth stage. A requisite of the spectral measurements was that measurements were taken when the plant material fully covered the soil background. For *Urochloa mosambicensis*, this requisite was only met when the samples were at the adult growth phase, and samples were therefore measured at this stage. A brief outline of the morphological characteristics and canopy features of the grass samples in the different growth stages is given below.

As seedlings the canopy of *D.eriantha* samples were tufted, erectile grasses standing approximately 15–25 cm high. This stage was equivalent to the green-up stage marking the onset of photosynthetic activity for new grasses, either at the start of a new growth season or following a burn and resprouting. As adults both *D. eriantha* and *U. mosambicensis* were without inflorescences and reached a maximum height of 70 cm. The tufts and the leaves of the adult *D. eriantha* samples were narrower than those of

the adult *U. mosambicensis* samples. This stage could be described phenologically as having reached maturity and full green-up. Morphologically the adult and flowering samples of *D. eriantha* did not differ in terms of leaf output, but at minimum two fully developed infloresences had emerged prior to taking the spectral measurements, of the flowering plants.

To invoke dormancy following flowering, the greenhouse conditions were altered. Samples were watered weekly, and the temperature was allowed to drop over-night to a minimum of 10°C. A sample was considered dormant when all the leaves had browned (i.e. no longer photosynthetic). Morphologically, the grasses sagged and the canopy opened thus exposing the soil background.

Field

An *in-situ* validation was used to test whether the studied algorithms were sensitive to phenological changes over time, by using spectra collected in the field. The outcome expected for this validation is that the developed algorithm would capture grasses, within a plot, advancing from one phenological stage to the next (e.g. for this study from adults to flowering or flowering through to dormancy).

Paired spectral samples of dominant grass species growing on the Northern Plains savanna system, Kruger National Park (KNP), South Africa, were collected. The dominant species in a plot was sampled once in the late wet season (late March- mid April 2007), and again in the early dry season (mid May - early June 2007), a minimum period of one month passed between each paired measurement. Using stratified point cluster sampling, 42 plots were sampled. Eight different grass species (*Bothriochloa radicans, Cenchrus ciliaris, Panicum* spp, *Setaria* spp, *Sporobolus ioclados, Schmidtia papphoroides, Themeda triandra* and *Urochloa mosambicensis*), were found to be dominant amongst these 42 plots. Two strata were defined based on a geological stratification that splits KNP into a granitic East and a basaltic West. The structure and phenological responses of the vegetation are influenced by the topography on these two substrates [Archibald and Scholes, 2007; Asner and Martin, 2009; Grant et al., 2000].

4.2.3 Spectral measurements

Greenhouse spectra

A laboratory set-up ensured a consistent method for the collection of spectra for all phenological stages. Spectra were collected using a GER 3700 spectroradiometer (Geophysical and Environmental Research Corp.), fitted with a 10° fore-optic. The radiometer was placed on a tripod at a 15° angle, and was fixed at 80 cm above the pot rim level. This created a field of view (FOV) of 14 cm in diameter (pot diameter was 19 cm). Mounting the spectrometer at this height allowed for the projected plant growth between the seedling and flowering growth phase of the grasses. The calibration panel (Labsphere, Inc, Sutton, NH), used to convert relative reflectance to absolute reflectance, was measured at a distance of 31 cm from the optic, creating a FOV of 5.5 cm in diameter. The calibration panel was 225 cm^2, and this FOV ensured an accurate reading of the panel. A halogen lamp was placed alongside the GER 3700 at the same level as the optic head.

Samples, when having reached their respective phenological development stages (see table 4.1), were transferred to the laboratory for measurement. A sample was fixed in position for a group reading, thereby ensuring the FOV was located directly over the pot centre. If needed, to ensure that the soil background was not included in the spectral measurement, the samples were first bunched together prior to taking spectral measurements. A group reading consisted of a reading of the calibration panel and a set of five separate measurements of the sample. To reduce directional effects, caused by leaf orientation within the canopy, the sample was rotated by 90° for each group reading [Cho and Skidmore, 2006; Mutanga et al., 2003], thus four group readings were taken per sample. The 20 spectra taken per sample were averaged to yield a single result.

Spectra were also collected of the soil background after the samples had been clipped, to determine if soils too could be discriminated from the vegetation using the respective algorithms.

Table 4.1: Plant age classes, the time taken until spectral measurements could be made and numbers of samples included in each class.

Code	Species	Phenological stage	Weeks from sowing	Samples
DES	*D. eriantha*	Seedling	5	21
DEA	*D. eriantha*	Adult	8	38
UMA	*U. mosambicensis*	Adult	10	27
DEF_{nl}	*D. eriantha*	Flowering	10	7
DEF	*D. eriantha*	Flowering	11	19
DED	*D. eriantha*	Dormant	16	39

$_{nl}$= samples that were treated with 0.05 % N per 1 kg soil. These samples flowered earlier and the spectra were therefore taken earlier than the remaining flowering samples.

Field spectra

In-situ grass canopy spectra were collected using a field spectrometer (Fieldspec Pro FR, Analytical Spectral Devices, Inc. (ASD)), fitted with an 8° fore optic. In line with the laboratory experiment it was ensured that soil background effects were minimised. Spectra were collected holding the optic between 80–100 cm from ground level, thereby creating a FOV in the range of 11–14 cm. The background effects could thereby be minimized, by ensuring the instantaneous field of view (IFOV) covered plant leaf material as much as possible. A calibration panel (Labsphere, Inc, Sutton, NH) was used in the spectral measures in order to convert radiange to reflectance.

In each plot a total of 25 spectra were collected from five separate plants of the dominant species found in that plot. The 25 spectra per plot were then averaged to create a single spectrum per plot. During the late wet season there were cloudy days, measurements were however taken under full sun. On unstable days (i.e. cloud and sun), high quality averaged plot spectra were obtained by collecting additional spectra. Prior to averaging, noisy spectra were deleted, but with the additional collected spectra, it was ensured that 25 spectra were used to create each plot spectrum .

Across the study area, 16 soil spectral samples were taken to capture the soil background variation across the study area. Each soil spectra was an averaged spectrum of 15 individual spectra collected at a site.

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Table 4.2: Age class range defined by the greenhouse experiment. Each class is defined as the inter-quartile range within each age category sampled in the greenhouse experiment

Age	CAI	PhIX	Samples
Soil	-1.59 – -1.31	-0.73 – -0.71	13
Seedling	-1.19 – -0.78	-0.70 – -0.66	21
Adult	-0.62 – -0.37*	-0.47* – -0.24*	65
Flowering	-0.74* – -0.42	-0.41 – -0.30	26
Dormant	1.31 – 1.63	-0.02 – 0.08	39

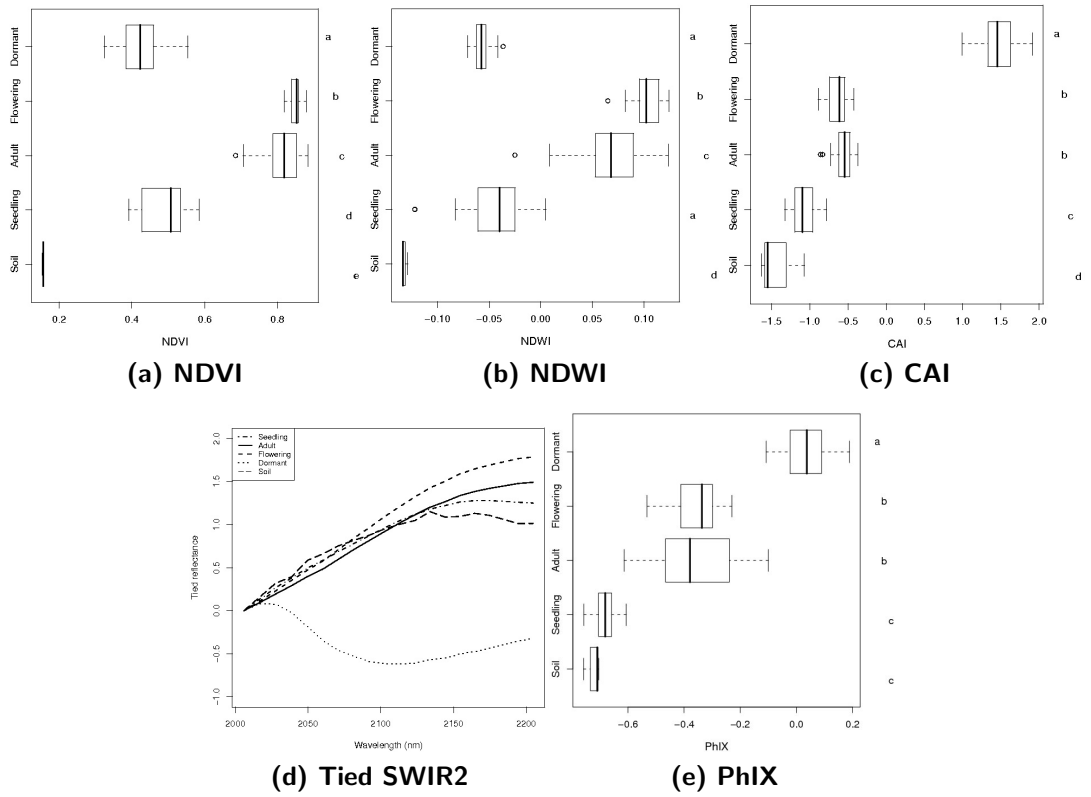
* = values combined to form the upper and lower class boundaries of the Adult class applied to the field dataset (see section 3.3).

4.3 Results

4.3.1 Algorithm comparison on the greenhouse dataset

The number of samples analysed for each growth stage is presented in table 4.1.

Both the CAI and PhIX algorithms met the requirement of chronological separation of phenology (figure 4.3c and 4.3e). For both these algorithms it was not possible to separate adult from flowering samples. All phenological classes differed significantly when applying NDVI (figure 4.3a), and for NDWI, all but the seedling and dormant classes could be statistically differentiated (figure 4.3b). For both NDVI and NDWI the order of phenological separation was not sequential, i.e. the values in the classes did not follow a correct chronosequence, e.g. from lowest values in seedling → adult → to the highest values for senescent.



(a) NDVI **(b) NDWI** **(c) CAI**

(d) Tied SWIR2 **(e) PhIX**

Figure 4.3: The statistical (Tukey HSD) separation (95% CI) out of different age classes grown under greenhouse conditions applied to 5 phenological algorithms: a) NDVI, b) NDWI, c) CAI, d) Tied SWIR2, and the newly proposed e) PhIX. For plots (a-c), and (e) the different letters on the right margin indicates that an age class differs significantly.

The SWIR2 tie method is not an index producing a single value, but rather discriminates image endmembers. In figure 4.3d the mean SWIR2 tied reflectance are shown for each phenological class. Visually the dormant samples can be easily discriminated, but the remaining classes are more difficult to separate from one another. From 2150–2200 nm the separation of the photosynthetic (i.e. seedling, adult and flowering) classes are phenologically chronological.

Given that the CAI and PhIX algorithms were the only two able to fulfil the requirement of chronological separation, only these two algorithms were applied to the field dataset. The value ranges applied to differentiate each phenological stage, for both the applied algorithms, are presented in table 4.2. In both the CAI and PhIX algorithms the adult and flowering class could not be statistically separated, these classes were combined to form a single class in classifying the field data (the values marked with an * in table 4.2 formed the boundaries for this class).

4.3.2 Algorithm application to the field dataset

The narrow ranges (table 4.2) created by the CAI algorithm for each of the age classes resulted in very few samples (8 out of 84 samples) of the field dataset falling into an age class, the majority of samples fell into the Transition or Senescent classes (table 4.3). The majority of the values created by applying the PhIX algorithm to the field dataset also resulted in samples falling into the Transition or Senescent class (57 out of 84), but the broader age class ranges of the PhIX algorithm resulted in the remaining 27 samples being classified into one of the original age categories.

In applying the algorithms to the field data it was expected that the phenological classes applied to the paired data would advance between the first and second paired reading. Eighteen and nine sample pairs remained unchanged between the paired seasonal measurement, when the CAI and PhIX algorithms were respectively applied. In analysing the actual output values produced, all 18 CAI values increased in value, thus in effect "ageing". Only six of the nine PhIX values advanced in value. Analysis of the remaining three PhIX samples showed that noise in the SWIR2 region and background soil impacted on the algorithms application. The single sample classified as Seedling in the CAI field dataset (table 4.3), was also

Table 4.3: Phenological classification of paired field data using the class ranges for the CAI and PhIX algorithm defined in table 4.2.

Age	CAI	PhIX
Soil	0	9^c
Seedling	1	6^c
Transition^b_{SA}	0	1^c
Adult^a	1	8
Transition^b_{AD}	75^c	43
Dormant	6	19
Senescent^d	17	14

^{a} = The Adult phenological class range was formed by a combination of the range of the Adult and Flowering ranges outlined in table 4.2; ^{b} = The Transition classes are defined by a sample that fell in the range between two age classes, where $_{SA}$ is the transition between the Seedling and Adult class, and $_{AD}$ is the transition between the Adult and Dormant class; ^{c} = These classifications include the classification results of 16 soil spectra taken in the field, i.e. for the CAI classification, all 16 soils were classified in the Transition_{AD} class; ^{d} = The Senescent class are any values that fall above the upper limit of the Dormant class.

a spectrum affected by noise levels in the SWIR2 region.

The soil samples from the field were all misclassified using the CAI algorithm, and were all classified into the adult to dormant Transition class. Nine of the 16 soil samples were classified into the Soil class (table 4.2) using the PhIX algorithm.

4.4 Discussion

The PhIX and CAI algorithms were capable of statistically and sequentially separating grasses of different phenological stages. NDVI and NDWI could statistically separate grasses into age classes, but because the separation was not sequential they could not be directly used for interpretation of grass samples in transition between different classes, e.g. an NDVI value of

0.65 (figure 4.3a and 4.3b) could be classified as either in transition between seedling → adult or adult → dormant.

Unlike the above algorithms, the tied SWIR2 method does not produce a single output value for interpretation. It has however been applied to phenological studies [Asner et al., 2000; Asner and Heidebrecht, 2002; Elmore et al., 2005], and was therefore considered to be a method that should be evaluated in this study. A visual evaluation of the tied spectra showed clear discrimination between photosynthetic and non-photosyn-thetic vegetation. What was less apparent was the discrimination between bare ground and photosynthetic vegetation (figure 4.3d). In the greenhouse study a single soil type was evaluated, but a broader range of soil endmembers might enhance this algorithms ability to discriminate soil and photosynthetic vegetation. This method could potentially be converted to create an algorithm for phenological discrimination, but in its current form it cannot be applied for direct interpretation of phenologic features.

In Nagler et al. [2003] different soils were shown to produce different ranges of values for the CAI algorithm. In this study a single soil type was used to define the soil class, but in the field a range of soils were sampled and these produced CAI values that fell out of the soil class range. The results here showed that the CAI algorithm could potentially be used to seperate out plants of variable phenological stages. It was also shown that soil variability impacted on interpretation of CAI values, and that this variability in combination with plant ages should be further investigated.

By developing the PhIX algorithm using continuum removed reflectance spectra, and area normalisation, an index was created that allows for comparisons of datasets collected in different seasons, under different solar conditions. Although the PhIX algorithm successfully differentiated grasses of various classes and soil, it showed a sensitivity to noise levels in the SWIR2 region. Effects due to noise in the SWIR2 region also impacted the application of the CAI algorithm. Solar irradiance has a pronounced effect on this spectral region [McCoy, 2005], and thus collection of spectra under overcast or hazy conditions should be carefully monitored as it will influence the effectiveness of these algorithms. The PhIX algorithm also showed that, at least in the dormant and senescent stage of phenologic development, it was affected by the presence of soil background. This effect on the algorithm should be further investigated, particularly with respect to mixed pixels, a common feature in arid and semi-arid environments [Okin et al., 2001].

Elvidge [1990] displayed the spectral progression of a number of trees and shrubs from green through to senescent. Visual evaluation of these spectra showed clear differences in both the VNIR and SWIR2 regions of the spectrum. Given that absorption features used in the PhIX algorithm are based on changes of pigments and development of the ligno-cellulose feature at 2100 nm, it seems reasonable that the PhIX algorithm could be successfully extended to a broad variety of plants.

Acknowledgements

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Chapter 5

Remote sensing of forage nutrients: combining ecological- and absorption feature data*

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Abstract

Forage quality in savanna and grassland systems determines the capacity of these systems to support ungulates [Jones and Wilson, 1987; Prins, 1996]. Findings from ecological and laboratory studies, focused on assessing forage quality, are combined to evaluate a remote sensing approach for predicting forage quality. Spatially available ecological findings (ancillary data), and physically linked spectral (absorption data) findings are evaluated and combined to predict forage quality (nitrogen, phosphorus and fibre concentrations). Ancillary data alone, could predict nutrients, with a higher goodness of fit, than absorption data (Ancillary: R^2_{adj} =0.42–0.74% compared with Absorption: R^2_{adj} =0.11–0.51). Species and soil were found to be ecological variables most frequently included in prediction models of ancillary data. Developing prediction models (through stepwise regression) with both ancillary and absorption variables did not necessarily result in significant models that include variables from both data types. Models for which both ancillary and absorption data were included, had the highest predictive capabilities compared to models where data sources were separate. This research provides an important step in the process of creating biochemical models for mapping forage nutrients in savanna systems that can be generalised over larger areas.

5.1 Introduction

Grassland-savanna ecosystems, support a high percentage of wild ungulate and domestic livestock populations [Jones and Wilson, 1987]. The importance of these systems, has led to extensive research into the properties that allow them to support these ungulate populations [du Toit, 2003; Werner, 1991]. A component of this research has targeted assessment of the quality of the food source; 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, 1990; Prins and Beekman, 1989]. Concentrations of different nutrients differ significantly between plant species [Jones and Wilson, 1987; McNaughton, 1988; Mu-

tanga 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., 2006a], 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 variability identified in forage quality nutrients, 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 managers or managers of wildlife reserves would benefit from a landscape quantification of forage quality. Collecting and analysis of forage, using wet chemistry techniques, is a time consuming and laborious task, this has been greatly aided 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 this spectral information, it is possible to map the distribution of plant biochemicals at a landscape level [Mutanga and Skidmore, 2004a; 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. This has not only been in savanna and grassland systems [Gianelle and Guastella, 2007; Mutanga and Skidmore, 2004a; Skidmore et al., 2010], but extensive work has also been undertaken in forest and cropping systems, where the assessment of nitrogen is 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]. What is evident in the results of these and other biochemical studies, is that absorption features that have been physically linked to foliar nutrient concentrations, were not the only wavelengths significant in the development of foliar nutrient models. In many of these studies additional wavelengths and spectral regions were identified as important to capture the variations in foliar nutrient concentrations [Cho and Skidmore, 2006; Mutanga and Skidmore, 2004a; Huang et al., 2004;

Johnson and Billow, 1996]. To create a reproducable model, the reason behind inclusion of variables in a model should be interpretable. All variables should ideally be physically or causally related to the item under study (e.g. for nitrogen, variables might include either known absorption features, or wavelengths linked to geological properties or phenology - which have been proven to result in nitrogen variations [Ferwerda et al., 2006a; Grant and Scholes, 2006; Owen-Smith, 2008; Skidmore et al., 2010]).

Most of the studies into quantifying the spatial distribution of biochemicals have been site-specific. The choice of including additional wavelengths, that have not been identified as having a physically link to a foliar nutrient, would therefore make sense if only a single measurement at a moment in time is desired, or if the wavelength link to the foliar nutrient is to be explored. If, however, it is the aim (and we believe it is) of remote sensing biochemical studies to provide algorithms that can be utilised, in multiple sites, at multiple moments of time, then variables in a model should be interpretable and transferable between sites and time periods.

In this study findings from ecological and laboratory research into forage nutrients are combined. These findings are transferred to remote sensing data, to evaluate if in unison, the quality of forage nutrients in a savanna can be predicted in an interpretable and transferable manner from remote sensing data. We believe the combination of this information would provide a sound platform for mapping and monitoring forage nutrients in these systems at a landscape level.

We first determined whether environmental factors that were significantly related to variations in forage nutrient concentrations, and available or potentially available as spatial data, could estimate forage nutrient concentrations (referred to as *ancillary variables* from hereon). The potential of spectral features, identified through NIRS that have been physically linked, to different nutrients, in predicting the forage nutrients, (referred to as *absorption variables* from hereon) were evaluated for predictive capabilities. Finally, we combined the ancillary and absorption variables to evaluate their combined ability to predict forage nutrients. 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 savanna sites.

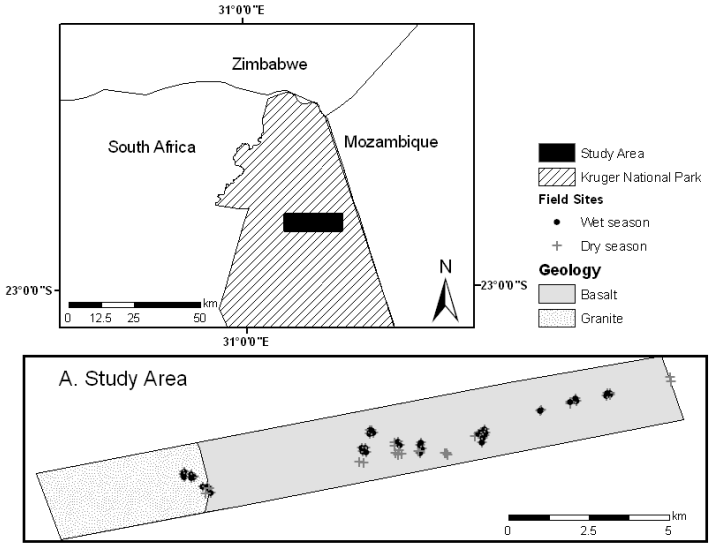


Figure 5.1: Location of field site within the Kruger National Park (KNP), South Africa. The inset shows the distribution of the plots, measured in the dry and wet season, stratified according to the underlying geology that splits the park into a granitic east and basaltic west.

5.2 Methods

5.2.1 Study Area

The study area was located on the Northern Plains of the Kruger National Park (KNP), South Africa (figure 5.1), the area is located between 22°49'S, 31°01'E and 22°44' S, 31°22'E, covering an area of approximately 25 x 6 km (inset figure 5.1). The location of the study area captures a geological transition, variation in fire treatments, and a rare game herbivore enclosure.

The study area is underlain by a geological complex dividing it into granites (west) and basalts (east) [Gertenbach, 1983](inset figure 5.1). The underlying geological complexes have implications for soil nutrient concentrations and consequently on the forage chemistry of the vegetation cover [Ferwerda et al., 2006a; 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 ver-

tic 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[1]" or "Roan Enclosure"), 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. Fire management within and without the enclosure has further contributed to the structural variation [Ferwerda et al., 2006a; Levick et al., 2009].

5.2.2 Data Collection

Field Sampling

Field sampling 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 (totaling 62 sites for the dry season).

The location of the field sites was defined in an earlier study by Mutanga et al. [2004a]. Mutanga et al. [2004a] defined the sites through a stratified clustered-random sampling. The area was stratified into open grasslands, mixed woodland and woodland. Using S-PLUS, x-y coordinates were randomly generated, plots were then located in the field using GPS (Garmin 12XL, with an estimated 3m accuracy). Purposive sampling included five samples on known natural salt licks. In the dry season of 2002, 96 sites were sampled, of these, 62 sites were re-sampled in the dry season of this study.

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

A plot of 15x15m was laid out at each GPS location. Within a plot, recordings were made of the estimated percentage tree, grass and bare ground cover. The dominant grass and tree species were recorded. Spectra were taken of the dominant grass species, and any other grass specie that was estimated to cover greater than 30% of the plot. Spectra were measured using a handheld ASD Fieldspec Pro FR spectrometer (Analytical Spectral Devices, Inc.). A minimum of five spectra were taken per plant (dependent on weather stability), and five plants of the same species were measured within a plot. Prior to spectral measurement of each plant, a spectra was taken of a calibrated spectralon panel (Labsphere, Inc, Sutton, NH), this allowed radiance measurements to be converted into absolute reflectance. Per measured species, per plot, the associated spectra were averaged to create a single spectral measurement.

Following spectral measurements, grass samples, of each species measured, 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 hours. Following drying, samples were ground through a 1 mm steel mill and transported back to The Netherlands for chemical analysis.

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 nutrients that we consider in this study are nitrogen, phosphorus and fibre. Nitrogen and phosphorus were analysed using a modified Kjedahl procedure, samples were initially digested in a mixture of sulphuric acid, selenium and salicylic acid [Novozamsky et al., 1983]. Digestion was then followed by colormetric measurement using a continuous flow analyser (SKALAR SAN plus). Fibre content (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).

Ancillary Variables

Ancillary variables that were either available or potentially producible from GIS or 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[2], 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. Phenological and Red Edge Position data were generated from spectra measured in the field. The species data collected in the field were used for analysis. 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]. A description of all the ancillary variable layers that were used in this analysis are presented in table 5.1.

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. 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 (chapter 3, table 3.3). 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 plants development. Within plants, phosphorus is primarily associated with plant

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

Table 5.1: 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, 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]. Across the site, three soil layers were classified.
Fire	Categorical	Frequency of fires over a five year period prior to sampling. Three classes were defined none, once and twice
Species	Categorical	Plant species sampled in the field. Eight separate species were identified. Additional species were sampled, however these were only identified in a maximum of two sites and were therefore combined to create a mixed species class. Thus in total this class has nine separate categories.
Phenology	Continuous	Phenological condition of a sample was generated using the spectral data collected in the field, and applying the PhIX algorithm defined in chapter 4.
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 defined by Cho and Skidmore [2006].

REP* = Red Edge Position.

Table 5.2: The wavelength absorption features selected for predictive analysis of the respective forage nutrients. 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, 1950, 1980, 2060, 2130, 2180, 2240, 2300, 2350
Phosphorus[b]	970, 990, 1450, 1490, 1530, 1540, 1580, 1780, 1900, 1940, 1950, 1960, 2000, 2080, 2100, 2250, 2270, 2280, 2320
Fibre[c]	1120, 1200, 1420, 1450, 1490, 1540, 1690, 1730, 1736, 1780, 1820, 1924, 1940, 1950, 2100, 2232, 2262, 2270, 2280, 2310, 2320, 2340, 2350, 2380

[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]

metabolic processes [Schachtman et al., 1998]. We have therefore chosen to spectrally associate 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 5.2.

5.2.3 Model development

Prior to model building all sample spectra were visually assessed for noise. 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. 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.

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 components analysis to these absorption feature wavelengths the collinearity between bands was reduced. These principal components (PC) were then input into the models. Within the ancillary variable, collinearity was found between variables that measured the same environmental parameters, e.g. the geological classes, soil 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].

Although stepwise regression is effective for developing multi-variate 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"[3] was implemented, for each forage nutrient, in each season, based firstly on ancillary variables, and then 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]. 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 nutrient, 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 nutrient concentrations, in

[3]Implemented in R [R Development Core Team, 2008], using the "leaps" (absorption) or "bestglm" (ancillary) packages [Furnival and Wilson, 1974].

Table 5.3: Results from the chemical analysis of the field samples. In the final column results of t-test's 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=6.50*** , df=53.62
Phosphorus	wet	0.1–0.5	0.2 ± 0.09	
	dry	0.1–0.4	0.2 ± 0.09	t=2.61**, df=82.46
Fibre	wet	34.1–49.7	41.4 ± 3.53	
	dry	35.8–51.1	43.4 ± 3.18	t=-2.88***, df=77.79

± the standard deviation of the mean; Significance level of t-tests, ***=0.99,**=0.95

each season. It was verified that the variables included in these final models were free from collinearity. Adjusted R^2 (R^2_{adj}) and root mean square error (RMSE) values are reported for the each of the selected models.

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 a forage nutrient. The results of this analysis allow us to provide suggestions as to a suitable approach to analyse forage nutrients in a heterogeneous savanna ecosystem.

5.3 Results

In agreement with earlier studies [Grant and Scholes, 2006; McNaughton, 1990] we found that forage nutrient concentrations differed significantly between the dry and wet seasons (table 5.3). The values for the different forage nutrients are comparable with those observed for this region [Grant and Scholes, 2006; Treydte et al., 2008].

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 5.4. All variables, included in these models, were significant contributors to explaining the respective concentration of forage nutrients.

Species, significantly contributed to explaining the concentration of forage nutrients, irrespective of the season. Soil type variables were also significant in their contribution to explaining differences in forage nutrient 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 nutrient content. The REP is only selected to estimate nitrogen concentrations, supporting the earlier findings of Cho and Skidmore [2006] and Mutanga and Skidmore [2007]. Phenology significantly contributed to explaining nitrogen, and fibre in the wet season (table 5.4).

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 on a continuous scale, that geological strata, in combination with soil strata, significantly contributed to explaining foliar phosphorus levels in the dry season.

Absorption Variables

The model variables, and predictive ability of models, developed with only spectral data (converted to PC data), associated with physical bond vibrations, is presented in table 5.5.

Absorption feature variables could better predict (higher R^2_{adj}) the concentration of a forage nutrient, when the forage nutrient levels were highest in the plant (e.g. nitrogen/phosphorus in the wet season) (table 5.3 vs table 5.5). Thirty four percent of the recorded variation in foliar phosphorus

Table 5.4: 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*", with all the variables included in table 5.1. All variables had a significant (p)-value less than 0.05.

Nutrient	Season	R^2_{adj}	RMSE (% DM)	Model variables
Nitrogen	wet	0.74	0.19	Aspect, Fire, Phenology, REP_c, Species
	dry	0.67	0.12	Phenology, REP_d, Sl_{ven}, Species
Phosphorus	wet	0.42	0.07	Sl_{knp}, Species
	dry	0.64	0.05	Geo_{ven}, Sl_{knp}, Species
Fibre	wet	0.70	1.94	Phenology, Sl_{knp}, Species
	dry	0.50	2.24	Species

* "Best subsets regression" implemented in R [R Development Core Team, 2008], using the "bestglm" library.

concentrations, was explained by using absorption features, associated with sugars and starch.

During the wet season water absorption features dominate vegetation spectra, these affects are particularly prominent in the SWIR region (1400–3000 nm) of the spectrum [Kokaly and Clark, 1999]. 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. Conversely in the dry season many of highest loadings associated with the selected PC's are associated with wavelengths found in the SWIR2 region.

Combined Data

A combination of absorption data and ancillary data did not always lead to forage nutrient models with higher prediction accuracies (table 5.6 vs Tables 5.4 and 5.5). Using the stepwise regression procedure, we found that in only half of the models which combined both sources of data, resulted in a parsimonious model with a higher R^2_{adj}. For the remaining models the ancillary variable models proved to be the most parsimonious model

Table 5.5: The significant principal components (PC) selected in the "best subset regressions*" 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 the PC.

Nutrient	Season	R^2_{adj}	RMSE (% DM)	Model variables(*)
Nitrogen	wet	0.45	0.27	PC2(910, 1020), PC4(640, even[a]), PC11(2180)
	dry	0.42	0.16	PC2(910, 1020), PC4(even), PC5(430, 460), PC9(2240), PC10(2060), PC11(2130)
Phosphorus	wet	0.34	0.08	PC2(970), PC5(1490, 2000), PC7(2320, even), PC8(2270)
	dry	0.24	0.08	PC2(970), PC7(2100), PC10(1530, even- 1490, 1540, 1580)
Fibre	wet	0.11	3.33	PC9(2262), PC14(1730,1736)
	dry	0.51	2.22	PC3(even), PC6(2232), PC8(2310), PC9(2310), PC10(2100)

* Best subsets regression implemented in R [R Development Core Team, 2008], using the "leaps" library.

[a] "even" the remaining wavelengths either listed or indicated, for a particular forage nurient (table 5.2). The "even" wavelengths had loading weights less that ± 0.5 but were similar in value.

selected. Similar to the result where only ancillary variables were used for modelling, we found that when combining ancillary and absorption variable, the species variable was again a significant contributor in all the selected forage nutrient models. Soil type data also significantly contributed to four out of the six forage nutrient models.

Model comparisons

Predicting the concentrations of any of the forage nutrients studied here, in either the wet or dry season, could be done with a higher degree of precision, using ancillary data alone compared to using only the absorption datasets

Table 5.6: Combined (ancillary+absorption) model variables. Model variables were selected through a stepwise selection procedure. The input variables were a combination of the best models from the ancillary (table 5.4) and absorption spectral data (table 5.5).

Nutrient	Season	R^2_{adj}	RMSE (% DM)	Model variables
Nitrogen	wet	0.74	0.19	Aspect, Fire, Phenology, REP_c, Species
	dry	0.70	0.11	PC2, PC10, REP_d, Sl_{ven}, Species
Phosphorus	wet	0.49	0.07	PC8, Sl_{knp}, Species
	dry	0.64	0.05	Geo_{ven}, Sl_{knp}, Species
Fibre	wet	0.70	1.94	Phenology, Sl_{knp}, Species
	dry	0.64	1.92	PC3, PC8, Species

(table 5.4 vs table 5.5).

A statistical comparison of the models (using AIC), showed that the six models finally selected in the combined data approach were the most suitable models (in terms of parsimony and predictive ability) for estimating forage nutrient concentrations (table 5.6). Only three of these models contained data from both ancillary and absorption spectral sources, the remaining three models were identical to the ancillary data models. The combined dry season fibre model was the only model of the six combined models that resulted in a reduction in the number of variables.

5.4 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 nutrients (nitrogen, phosphorus and fibre) remote sensing derived variables - based on ecological and spectroscopic theory, that predict each of the respective forage nutrients in both the dry and wet season. These variables, could be used as a base from which to generate algorithms, for estimating forage nutrient content in savanna regions.

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

For all forage nutrients, 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 a significant variable in explaining nurient variations in different seasons.

In this study, species information was not derived from remote sensing data. 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, 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 seperability of species [Ribeiro da Luz 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.

Absorption features associated with fibre are all located in the SWIR region of the spectrum (table 5.2). During the wet season the SWIR region is strongly affected by water absorption features [Elvidge, 1990; Kokaly and Clark, 1999], therefore the cellulose and lignin features are masked by water features. Our results show that during the wet season fibre is better estimated through ecological features that explain the environment (soil type), and plant morphology (phenology and species). During the dry season when cell water content is negligble, then the SWIR features of lignin and cellulose can be used to predict the concentration of fibre.

Soil, significantly explained variations in the phosphorus concentrations in both the wet and dry seasons (table 5.4). 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 classifica-

tion system [Macvicar et al., 1977], as this classification system details the catenal soil strata.

For nitrogen, if only environmental variables were considered, then plant phenology and REP, in addition to species, were significant contributors in both seasons (table 5.4). 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, phytomass [Darvishzadeh et al., 2008c,b; 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., 2008c; Grossman et al., 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 nutrient concentrations. The wavelengths (as highest loadings in the PC) attributed to predicting the forage nutrient 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 terms of creating generalisable algorithms for predicting forage nutrient concentrations in savanna grasses, this research showed that, while a base algorithm can be defined for each forage nutrient, 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.

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 layer of data that are created in association with a relevant variable, 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 selected 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].

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.

5.5 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.

2. Species and soil information were two ecological variables that repeatedly (temporally and between forage nutrients) significantly contributed to the estimation of forage nutrients.

3. Ancillary data could model forage nutrient concentrations with higher goodness of fit, in both the wet and dry seasons, than absorption data alone.

Acknowledgements

The authors wish to thank the Kruger National Park, for the opportunity to conduct this research. KNP Scientific Services for logistic support, the Shingwedzi staff, and in particular the game guards (Onnica Sithole and Wilson Dinde) for accompanying the researcher in the field. To the Department of Animal, Plant and Environmental Sciences at the University of Witwatersrand for the use of their grinding mills. To Anne-Marie van den Driessche, Resource Ecology Group, Wageningen University for her assistance in chemical analysis of the plant samples. David Rossiter, ITC, University Twente, for suggestions and clarification of statistical procedures used in this study.

Chapter 6

Mapping savanna forage quality, in the dry season *

*This chapter is based on the following paper: Knox, N.M., Skidmore, A.K., Asner, G.P., Prins, H.H.T., van der Werff, H.M.A., de Boer, W.F., van der Waal, C., de Knegt, H.J., Kohi, E.M., Slotow, R., Grant, C.C.. Mapping savanna forage quality, in the dry season, using CAO Alpha imagery. In preparation, *Remote Sensing of Environment*.

Abstract

Forage quality within an African savanna would be well described in terms of nutrients that are limiting (nitrogen and phosphorus) and nutrients that constrain the intake rates (non-digestible fibre) of herbivores. These forage quality nutrients have been shown to be particularly crucial in the dry season when concentrations of limiting nutrients decline and non-digestible fibres increase. Using artificial neural networks, in this study, we test the ability of a new imaging spectrometer (CAO Alpha sensor), in combination with ancillary data, to map quantities of grass forage nutrients in the early dry season within an African savanna. Respectively 65%, 57% and 41%, of the variance in fibre, phosphorus and nitrogen concentrations can be explained. We found that all forage nutrients show response to fire. Principal components analysis, not only reduced over-fitting in neural network models, but was a useful method for removing cross-track illumination effects in imagery. To further improve the mapping of forage nutrients in the dry season we believe that spectra within the SWIR region, or additional relevant ancillary data, are required.

6.1 Introduction

Within African savanna ecosystems, phosphorus and nitrogen have been identified as limiting forage nutrients in the diets of grazers [McNaughton, 1990; Prins, 1996]. To maintain an energetic balance, a grazer needs to obtain sufficient quantities of required forage nutrients before reaching their digestive system intake constraint for non-digestible fibre [Grant et al., 2010; Treydte et al., 2009; van Soest, 1996]. With the use of modelling within African savannas, it has been shown that during the dry season, ungulates were unable to meet their nutritional nutrient requirement needs prior to reaching the gut intake constraint [Treydte et al., 2009].

At landscape scale, forage nutrient levels will vary in response to multiple factors (e.g. edaphic, rainfall gradients, fire, herbivory), creating a patchy distribution of nutrients [Grant and Scholes, 2006; Prins and van Langevelde, 2008a; Treydte et al., 2007]. Having an overview on this distribution would be valuable input for effective management, particularly at a time when these nutrients are limited. Remote sensing has the potential

to rapidly, record these variations across large areas.

It has been demonstrated that forage quality nutrients (nitrogen, phosphorus and tree condensed tannins) could be mapped, during the wet season in an African savanna system, using hyperspectral data [Ferwerda, 2005; Mutanga and Skidmore, 2004a; Mutanga and Kumar, 2007; Skidmore et al., 2010]. Although not creating maps, Mirik et al. [2005] demonstrated the potential of hyperspectral data to estimate forage nutrient values in rangelands on an areal basis ($g.m^{-2}$). During the dry season, vegetation structure changes which in turn results in spectral changes of vegetation [Elvidge, 1990; Kokaly and Clark, 1999]. Elvidge [1990]; Asner [1998] and Asner et al. [2000] highlighted some of the changes that take place in various vegetation types as vegetation dries and becomes senescent (e.g. change of red edge shoulder, increase in prominence of SWIR features associated with lignin and cellulose). Here, we explore whether these changes in optical properties allow for the prediction and mapping of forage nutrients, during the dry season. This is tested using CAO Alpha hyperspectral imagery obtained from a flight campaign that took place over the Northern Plains of Kruger National Park (KNP) in May 2008 (i.e. early dry season).

The Carnegie Airborne Observatory (CAO) Alpha sensor[1] is a new airborne system which integrates hi-fidelity imaging spectrometer and LiDAR. Previous mapping of plant nutrients within the KNP used HyMAP imagery, covering a spectral range from 500–2450 nm. The neural network algorithms implemented for mapping of plant nutrients by Mutanga and Skidmore [2004a]; Mutanga and Kumar [2007] and Skidmore et al. [2010] all included selected input wavelengths from the VNIR and SWIR regions. The CAO Alpha sensor covers a spectral range from 367–1058 nm, therefore wavelengths within the SWIR regions are not available for modelling.

To account for limitation of nitrogen and phosphorus in African savannas [McNaughton, 1990; Prins, 1996], and gut constraint size with respect to quantity of non-digestible fibre consumed [van Soest, 1996], ideally concentrations of all three of these nutrients should be considered when analysing forage quality in an African savanna [Treydte et al., 2009]. Earlier work in imaging spectroscopy has focused on mapping nitrogen and phosphorus [Mutanga and Skidmore, 2004a; Mutanga and Kumar, 2007; Skidmore et al., 2010], but to the authors knowledge, none has looked at mapping

[1] cao.stanford.edu/

fibre. Work in agriculture has produced methods to rapidly assess fibre content using NIRS and field spectroscopy [Albayrak, 2008; Kawamura et al., 2008; Starks et al., 2004], but this has not been upscaled through to image level. In this study we investigate three aspects to nutrient mapping: We firstly consider mapping three separate nutrients, which when considered together provide ecologists and farmers, with a complete overview of the grazing forage quality resource. Secondly this investigation is conducted in the dry season, an important time for herbivores when nutrients are limited, and a time when optical properties of vegetation are influenced by increased cover of non-photosynthetic vegetation. The third component of this study considers the potential of CAO Alpha imagery for mapping savanna grass forage quality (nitrogen, phosphorus and fibre) during the dry season. Created maps are discussed in terms of whether they make ecological sense, the implications for dry season forage nutrient mapping, and the potential of the CAO Alpha imagery for mapping each of the forage nutrients is discussed.

6.2 Methods

6.2.1 Study area

The study area was located on the northern plains of the KNP, South Africa. The focus study area (top left: 22°45'47"S, 31°14'42"E; bottom right: 22°47'15"S, 31°17'30"E) fell within a larger extent (West: 22°46'S and 31°11'E; East: 22°46'S and 31°21'E) covered by a HyMAP image acquired in March 2003 (wet season) (figure 6.1). The area was located on the basaltic plains, which are characterized by high grass production and a woody layer dominated by mopane (*Colophospermum mopane*) shrubs. The soils are rich in iron- and magnesium- containing minerals, that easily erode forming dark clay soils [Grant et al., 2000]. A drainage line runs through the study area creating a vlei (wetland) grassland.

The focal study area included the 304 ha N'washitsumbe roan enclosure[2] (figure 6.1 inset). This rare-game enclosure was established in 1967 (and extended in 1984 by 48 ha, to include vlei grassland), to act as a breeding enclosure for roan antelope (*Hippotragus equinus*). All other large herbi-

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

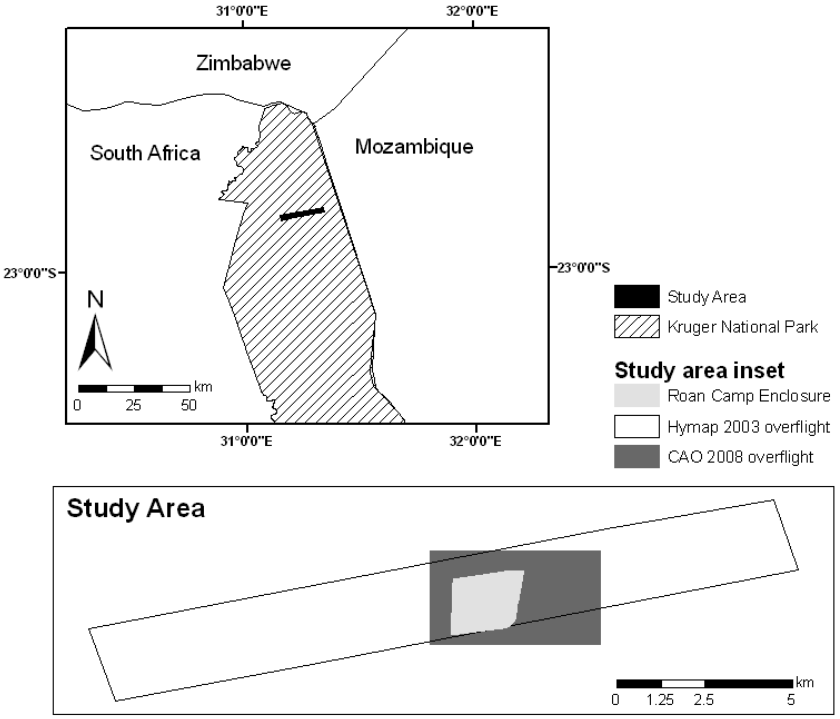


Figure 6.1: Location of the study area within the KNP. The inset shows the study area, defined by the overflight of the HyMAP image acquired in 2003, the location of the focus study area, defined by the CAO Alpha overflight extent, and the extent of the N'washitsumbe roan enclosure within these areas.

vores (greater than ±5 kg) and predators were excluded. The enclosure is structurally distinct from its surroundings with a greater structural diversity of the woody vegetation within the enclosure compared to outside [Asner et al., 2009; Levick and Rogers, 2008]. Trees have been associated with increases in nutrient concentrations [Ludwig et al., 2004; Treydte et al., 2008]. Fire has been an important management tool used within the park [du Toit et al., 2003]. The management of fire within the enclosure differs from the surroundings. Areas are burnt at different time intervals, resulting in a spatial patchwork of fire frequencies across the study area. Fire, grazing, trees and soils have all been attributed to variations in nutrient levels [Allred and Snyder, 2008; Archibald, 2008; Craine et al., 2009], making this site ideal for testing the potential of remote sensing for mapping nutrient

variability within a savanna system.

6.2.2 Image acquisition

On 1 May 2008, using the CAO Alpha system, imagery was acquired over the focus study area. Data were collected from 2000 m above ground level, providing imagery with a spatial resolution of 1.12 m. To cover the focus area, a total of 9 flight lines were required. The overflight took place within 2 hr of solar noon. The spectral resolution of the imagery was 9.4 nm covering the spectral range between 384–1054 nm, creating an image with 72 contiguous bands.

In this study, only the imaging spectrometry data from the CAO Alpha system were used. Pre-processing of the image data was automated and integrated with the LiDAR and GPS-IMU components of the system. In this section, only the pre-processing of the image data are described, but for a more comprehensive description of the entire system processing see Asner et al. [2007]. The image data were converted to at-sensor radiance by using radiometric corrections developed during sensor calibration at the laboratory. The apparent surface reflectance was derived from the radiance data using an automated atmospheric correction software (ACORN 5 Li-Batch; Imspec). The atmospheric model requires multiple inputs, some of which were estimated and the rest derived from the integrated data: from the LiDAR (elevation), GPS-IMU (aircraft altitude), atmosphere type, and estimated visibility. ACORN software used a MODTRAN look-up table to correct for Rayleigh scattering and aerosols. Water vapour was estimated from the imagery using the 940 nm absorption feature. The image data were delivered as an end product of the nine image strips mosaicked, and ortho-registered to within 0.4 m absolute error into a single output image.

6.2.3 Field sampling

Field samples were collected within a two week period around the time of the overflight. Twenty field sites, defined (stratified random clustering) in an earlier study by Mutanga et al. [2004a], that fell within the boundaries of the focus study area were sampled. An additional 10 sites were included as random samples within the study area strata. These sites were selected

to capture the variation in fire frequency and soil strata. Figure 6.2 shows the location, of the sampled field sites across the study area, the location of the rare game enclosure is included for reference (figure 6.2a). The field site locations are shown in respect to the soil strata (figure 6.2b) and fire frequency strata (figure 6.2c). Although savannas are a combination of tree and grass layers, we focus here on the grazing resource and thus only grass samples were collected for analysis.

Sites were located using a GPS receiver (Garmin 12XL, estimated accuracy of 3 m). At these sites a 15 x 15 m plot was laid out. The percentage vegetation- and bare ground cover and dominant grass and tree species were recorded. Using an ASD Fieldspec Pro FR field-spectrometer (Analytical Spectral Devices, Inc.), field spectra of the dominant grass species that covered an area greater than 30% of a plot, were measured. Five spectra were taken per plant, and a minimum of five separate plants of a species were measured in each plot. The number of spectra taken was increased when the plants appeared to differ structurally. Before each plant was measured, the spectral reflectance of a calibration panel was taken (Spectralon, Labsphere, Inc, Sutton, NH). This allowed the spectra to be converted to absolute reflectance. In each plot, following spectral measurements, grass samples (minimum five plants) for each species were clipped, pooled, and bagged for drying and later chemical analysis. A total of 52 plant samples were collected for chemical analysis.

6.2.4 Chemical Analysis

Grass samples were dried at 70°C for 48 hr, in an oven. The dried samples were mill ground to 1 mm using facilities at the Agricultural Research Council, Nelspruit (ARC). These dried and ground samples were transported to Wageningen University, The Netherlands for chemical analysis.

For determination of nitrogen and phosphorus concentrations, a modified Kjeldahl procedure was used. Samples were initially digested in a mixture of sulphuric acid, selenium and salicylic acid [Novozamsky et al., 1983]. Following digestion, the samples were colorimetrically measured using a continuous flow analyser (SKALAR SAN plus). Fibre (Acid Detergent Fibre - ADF) concentrations were determined according to the ANKOM filter bag procedure, using an ANKOM $^{200/220}$ fibre analyser (ANKOM

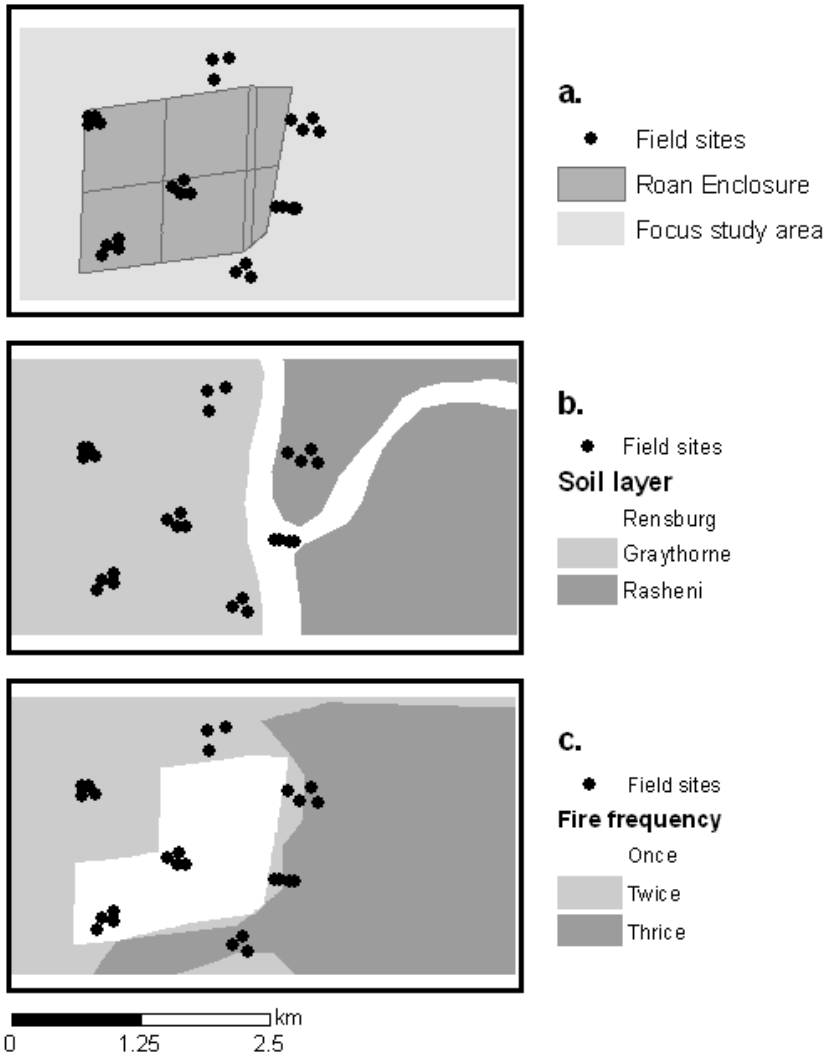


Figure 6.2: Ancillary GIS data used in the network models: a) The focus study area with the demarcation of the N'washitsumbe enclosure and the position of the field sites. b) The soil strata across focus area, with the field sites overlain. c) The frequency of burning between the imagery acquired in 2003 and the imagery acquired for this study.

Technology, Macedon, NY, USA).

6.3 Data Analysis

6.3.1 Selection of modelling method

Using linear modelling, Mirik et al. [2005] did not find any relationship between spectra and biochemicals measured on a dry matter basis. Mutanga and Skidmore [2004a]; Mutanga and Kumar [2007] and Skidmore et al. [2010] demonstrated that with the use of non-linear modelling, significant relationships existed between spectra and biochemicals measured on a dry matter basis. Savanna systems typically have a mix of photosynthetic (PV) and non-photosynthetic vegetation (NPV), irrespective of season. Asner [1998] determined that variances in PV:NPV cover were non-linear. A possible reason therefore for the effectiveness of the non-linear modelling, compared to linear modelling, is its ability to capture this variance in standing cover of PV:NPV within the savanna systems. Given the *a-priori* knowledge that the vegetation would be mix of both photosynthetic and non-photosynthetic states, and the earlier success in nutrient mapping, using non-linear methods, shown by the above authors, it was decided to apply non-linear modelling in this study.

Neural networks are capable of using high dimensional data, from multiple sources, without being constrained by statistical distributions [Atkinson and Tatnall, 1997]. Although this capability is useful when causal features for predicting a feature are unknown, it does have some constraints. Neural networks are "black boxes", therefore implementation of trained models to completely new datasets is not possible [Skidmore et al., 1997]. As the number of input variables in a neural network increases, an increase in computational time to train the network is required [Skidmore et al., 1997], increases the number of samples required to train the network [Atkinson and Tatnall, 1997], and often results in a network which is unable to generalise to new data. Causal features for predicting biochemicals with spatial data could include known absorption features within spectra, or ancillary GIS layers of environmental factors. Whether these causal features alone are sufficient for predicting forage nutrients in the dry season is evaluated using various input types for neural network modelling.

In this study the networks are tested for the ability to accurately generalise to a validation dataset. The networks are trained using three possible input datasets: Spectral data is included either as the full CAO Alpha spectrum (full dataset), or as a spectrum with the collinearity between wavelengths removed (generated through applying a principal components analysis), or as a causal spectrum of selected wavelengths associated with known absorption features (causal dataset). The spectral dataset is combined with ancillary data layers (GIS and RS products) to create the input data to be fed into the neural networks. From the generated models, the best fitting networks for each nutrient are selected, these are then inverted and applied to the full image range to create nutrient maps across the savanna landscape.

6.3.2 Data processing for model input

Imagery:

The mosaicked image had clear cross-track illumination effects. These effects were minimized, by per pixel, fitting a convex hull across the spectral range, the reflectance spectrum was subtracted from the hull resulting in a continuum removed spectra. This procedure allowed spectral features associated with the nutrients of interest to be maintained [van der Meer et al., 2001]. For the remainder of the analysis the first two and last two bands were dropped, these bands were dropped because they equalled 1 (a result of continuum removal). Sixty-eight bands were therefore retained for input into training the network models.

Ancillary data:

Ancillary data, if related to nutrient concentration variance, can aid model prediction (chapter 3, Mutanga and Skidmore [2004a]). Within the study area (chapter 3 and 5), during the dry season, we found that phenology, soil, species, and geology were all variables that related to nutrient level variance. Ferwerda et al. [2006a] showed that fire frequency had a significant negative effect on grass growth, and Skidmore et al. [2010] showed interaction effects between fire and parent material on foliar nutrient variations. Based on

these findings, we assessed whether these variables identified above could be included as input variables for the network modelling.

To capture the variation in plant age across the landscape, a phenological algorithm was applied to the data. Ideally either the PhIX (section 4.2.1, chapter 4) or CAI [Nagler et al., 2000] algorithms would have been used, but the available spectral range of the CAO Alpha imagery prevented this. Given the season (dry), and no recent fires in the area and therefore no grasses in an early growth phase, it was considered that using the normalised area under the visible curve (section 4.2.1, chapter 4) was a suitable means to evaluate plant age variations (termed *phenology* hereafter).

Using the soil classification system based on the South African soils classification system [Macvicar et al., 1977], three different soil types were identified in the focus study area (figure 6.1b). The underlying geology was uniform [Venter, 1990], and therefore this layer was excluded.

Different plant species have been linked to the type, location and translocation of forage nutrients in plants [Chapin, 1980]. In chapter 5 we showed that inclusion of a plant species variable was a significant variable in generated models for explaining variations for all three forage nutrients analysed in this study. This we believe is a valuable layer to include in modelling, however no plant species map of this area exists and thus a plant species layer could not be included.

As fire plays a role in differences in forage nutrient levels, then this may be apparent between two different measurements in time. Using the time frame between the 2003 HyMAP, and the CAO Alpha imagery used in this study, the frequency of burning was determined. GIS data on annual fire occurrence between 2003–2008 was obtained from the GIS/remote sensing centre[3], Scientific Services, KNP. These GIS data layers were combined and used to develop a layer of fire frequency within the focus study area. Three fire frequency levels were identified (figure 6.1c). The area burnt once was burnt only in the 2004–2005 fire season, the area burnt twice was burnt in the 2002–2003 and 2004–2005 fire season and the area burnt on three occasions was burnt in both these seasons and in 2006–2007.

Phenology, fire frequency and soil type were the three ancillary data layers that were combined with spectral data as input for the network models.

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

Normalisation:

Skidmore et al. [1997] demonstrated that normalising input layers to a network reduced the number of epochs required to train network models, and increased the training accuracy of models. Input and output layers were normalised using a linear contrast stretch.

Defining the output and validation datasets:

In order to create a model that can be generalised, it is necessary that the dataset used to train the model covers a broad range of values in the output layer and that the variability associated with the output layer is captured within the input layers [Atkinson and Tatnall, 1997].

The field sites sampled were 225 m^2, with an image spatial resolution of 1.12 m, 178 pixels were located within each field site. Pixels for the development of the models were individually selected at the location of the 30 field sites. Pixels were selected based on the percentage cover by an individual species (percentage cover was a component of the collected field data) and a visual comparison with the field spectra collected at each site (see section 6.2.3) and the image spectra. In total 448 pixels distributed between the different sites were selected. These 448 pixels covered the breadth of the nutrient concentrations measured in the grass samples. Of these 24 pixels were withheld and used for model validation. The 24 pixels were randomly selected, but it was verified that they covered the nutrient ranges covered in this analysis. The remaining 424 pixels (and their associated nutrient concentration) were used in developing the neural networks.

6.3.3 Neural network implementation

Modelling inputs:

Three inputs were generated to model the forage nutrients:

1. *The full range* - The three ancillary data layers and the 68 layers from the continuum-removed CAO spectral dataset were stacked to create a 71 node input layer.

2. *The reduced range* - the 68 band, continuum-removed CAO Alpha spectral dataset was run through a principal component analysis. Using a combination of the eigenvalues and eigenvectors, the first five principal component layers were selected. These layers accounted for 98% of the variation within the CAO Alpha data. Visualisation of the principal components also showed that above the fifth component traces of the cross-track illumination were evident. This gave further support to the inclusion of only the first five components. Together with the ancillary data a stack of 8 nodes was created for this input layer

3. *The causal range* - A literature study revealed that, within this spectral range, there were absorption features associated with variations in nitrogen concentration (see Knox et al. [2010]). Wavelengths located at 422, 432, 460, 639, 715, 724, 913 and 1016 nm [Curran, 1989; Mutanga et al., 2004c] were identified and these were used in combination with the three ancillary data layers as input for a nitrogen prediction model, creating 11 nodes for the input dataset.

Given no causal absorption features were identified for phosphorus and fibre within the CAO Alpha spectral range, network modelling was applied using only the full and reduced spectrum range data as input for modelling.

Model training and selection:

A 3-layer back propagation perceptron network, based on the algorithm of Rumelhart et al. [1986] was implemented (programmed in ENVI\IDL®). Unlike widely used linear empirical methods (e.g. stepwise regression), the implementation of neural networks is stochastic and requires an iterative process to select the best models. Networks are prone to over-learning, resulting in over-fitted models and models that are unable to generalise to new datasets [Chen et al., 2007; Skidmore et al., 1997], therefore the use of a test and training set for model evaluation is essential. The most challenging aspect to applying neural networks is to determine the models that are best suited to predicting the item of interest. Using a similar procedure applied by Mutanga and Skidmore [2004a] and Skidmore et al. [1997], we trained and tested our models. This procedure for training the models is outlined in figure 6.3.

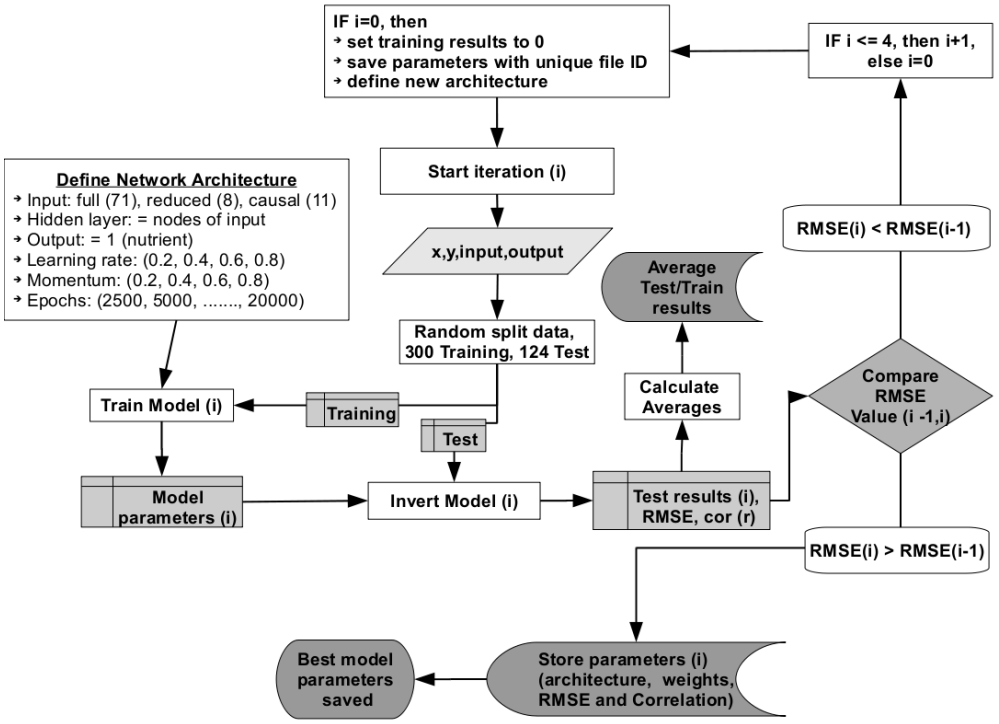


Figure 6.3: The procedure implemented for training and saving the best individual network parameters. For each nutrient, the model outcomes were evaluated per input data type, the model that produced the lowest average test RMSE value was selected as the best-input model. These different best-input models were compared and the model with the lowest test RMSE value was selected as the best model for inversion. For each network architecture tested, five iterations (i) were run.

Once all the individual components of the network architecture had been trained and tested, the network with the lowest average RMSE value obtained for the test and training dataset, for each nutrient, and each input data model was selected. Given the stochastic nature of neural networks, model selection is a compromise between several factors (network architecture and the training and test results) [Skidmore et al., 1997]. Taking this property into consideration, if two outputs had the same lowest average RMSE value, then the network with the least number of epochs required for training the models was selected. For each nutrient the different selected models were compared, and the model with the lowest test RMSE value was selected as the model for inversion.

Model inversion and validation:

The selected model for each nutrient was inverted and used to create an output map. The network architecture, training set size and training time (epochs) are all factors that contribute to the ability of a network to interpolate and extrapolate on new data-sets [Atkinson and Tatnall, 1997]. As stated earlier this study focused only on the grazing resource, network training was therefore limited to grass samples. The pixels selected for training the models were limited to pixels containing grass spectra. The savanna environment is however a combination of trees, grass and bare ground. To limit extrapolation beyond the values used to train the model, a check was performed prior to inversion. Inversion was performed on a pixel by pixel basis. It was first verified if each layer within a pixel fell within the same spectral range used to train the models, only if this was the case, for all of the layers, was model inversion applied. Each output map was recalculated to the percentage value of the nutrient, by inverting the linear contrast normalisation.

Using the 24 pixels set aside for validation, the output images were validated, the root mean square error (RMSE) and R^2_{adj} of these images are presented.

Table 6.1: Summary of the chemical analysis of the 52 plant samples collected in the field.

Nutrient	mean (% DM)	Range (% DM)
Nitrogen	0.53	0.31–0.91
Phosphorus	0.17	0.04–0.36
Fibre	44.7	40.9–48.5

6.4 Results

The results from the chemical analysis performed on the sampled plants is presented in table 6.1. The range of nitrogen and phosphorus is in agreement with findings reported by Grant and Scholes [2006]. The findings of Grant and Scholes [2006] and Treydte et al. [2009] indicated that nitrogen and phosphorus, in this region, during the dry season, fell below maintenance levels required by herbivores. Of particular interest is that the mean nitrogen and phosphorus levels were already, so early in the dry season, below levels identified for maintenance for wild herbivores. Nitrogen maintenance levels for wild herbivores has been calculated as 1% N on a dry matter basis [Prins and Beekman, 1989], and phosphorus maintenance levels have been calculated for wild equids to be 0.24% P on a dry matter basis [Duncan, 1992].

The quantity of standing biomass contributes to a pixel's signal [Asner, 2004]. To ensure predictions were related to the nutrient content and not standing biomass, they were compared with leaf area index measurements (LAI). LAI measurements were collected in a separate study (unpublished data[4]), and those measurements confirmed that the forage nutrient values and LAI values were uncorrelated (r-values below 0.01 for the three nutrients).

6.4.1 Network architecture

The neural network parameters selected for each of the input data sets (*causal, full* and *reduced*), per nutrient, are presented in table 6.2. What is

[4]Filiz Bektas Balic, Istanbul Technical University, Turkey

evident from the selected models is that there is no ideal network architecture that applies either per input dataset or relative to each nutrient. For each nutrient the use of the entire spectral range as input resulted in the lowest test RMSE. The inclusion of known causal bands did not result in better fitting models, compared to either the entire spectral dataset or a reduced spectral dataset. The lack of consistent patterns (e.g. more input would need more epochs) observed in reaching the final selected models highlights the stochastic nature of neural networks [Skidmore et al., 1997]. Similar to the findings of Uno et al. [2005], we found that there was little difference between results using the principal components and the entire spectral dataset, the processing time for both datasets was also similar.

Table 6.2: The selected network architectures, for the three forage nutrients tested. Selection of a model was made by selecting the network models that produced the lowest RMSE values when the trained models were tested (figure 6.3).

Nutrient	Input Data	L/N[a]	LR[a]	M[a]	Epochs	Training R^2	Training RMSE[b]	Test R^2	Test RMSE[b]
Nitrogen	Full	71	0.8	0.6	17500	0.79	0.004	0.49	0.123
	Reduced*	8	0.2	0.2	15000	0.53	0.01	0.53	0.161
	Causal[c]	11	0.2	0.8	15000	0.55	0.006	0.34	0.195
Phosphorus	Full	71	0.2	0.2	5000	0.88	0.005	0.74	0.14
	Reduced*	8	0.4	0.6	12500	0.79	0.007	0.72	0.143
Fibre	Full	71	0.8	0.4	15000	0.96	0.004	0.67	0.184
	Reduced*	8	0.4	0.4	10000	0.64	0.01	0.62	0.19

[a]= L/N - The number of input layers and neurons in the hidden layer; LR - Learning Rate; M - Momentum

[b]=The RMSE values are unit-less as they are based on normalised values used for training the network and not the original percentage values for each nutrient.

[c] = The wavelengths used in the causal dataset were 422, 432, 460, 639, 715, 724, 913, 1016 nm [Curran, 1989; Mutanga et al., 2004c].

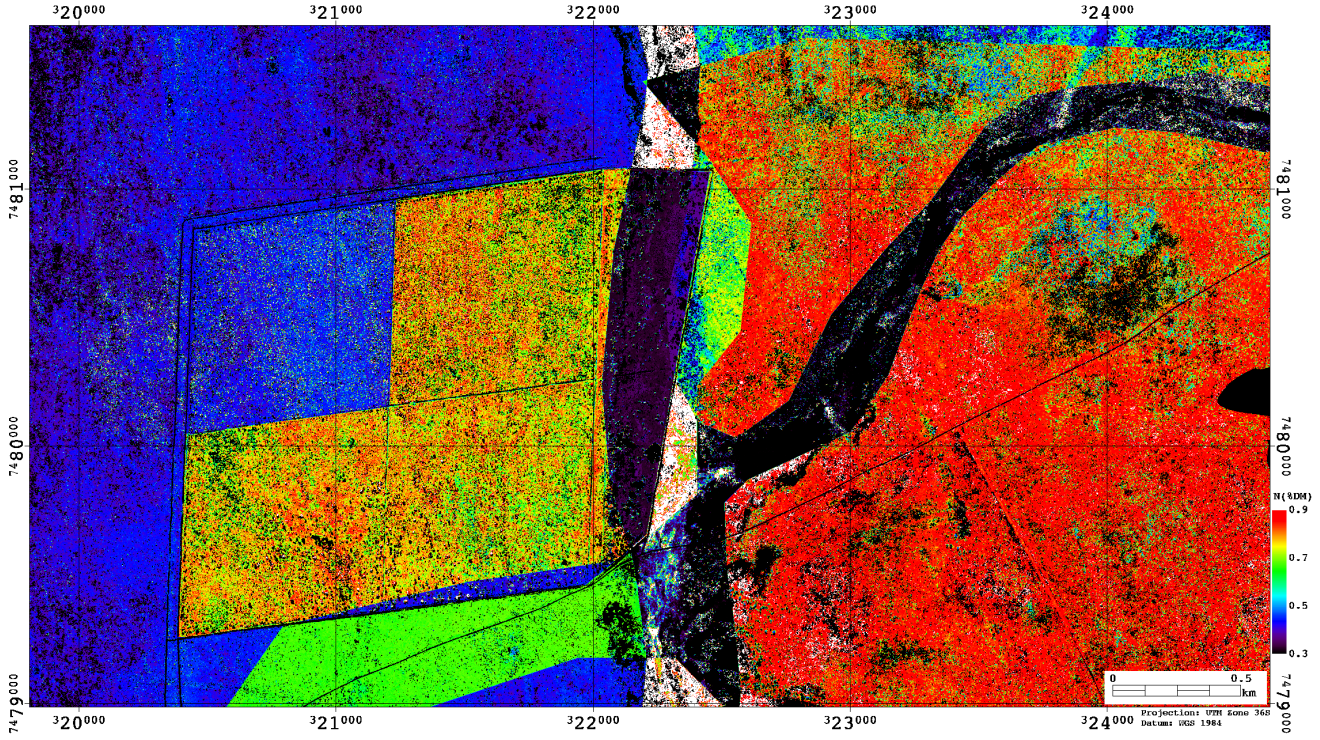
* the network model selected for inversion to create the nutrient maps shown in figure 6.4

6.4.2 Network inversion and validation

In section 6.3.3 it was stated that the models with the lowest test RMSE values would be selected for inversion. Thus, for phosphorus and fibre the models using the full dataset was selected for inversion and for nitrogen the reduced model (principal components) was inverted (table 6.2). In section 6.3.2, it was reported that the mosaicked CAO Alpha imagery contained cross-track illumination effects. By applying continuum-removal to the mosaicked image, it appeared that these effects were removed. However, when the fibre and phosphorus images were inverted to produce maps of nutrient concentrations there was some visual evidence of the cross-track illumination artefact in the output image. These effects were not evident when the principal component models were inverted to create nutrient output maps. None of the validation points were located on or neighbouring a mosaic line, therefore it was not possible to test the effect of these illumination differences, however, visually it appeared that the illumination artefacts affected the nutrient predictions. The test results between network models trained using the full dataset and the reduced dataset were small; hence it was decided that using the reduced models for inversion was an appropriate choice, thereby minimizing the illumination artefacts. The resultant images produced by model inversion are shown in figure 6.4.

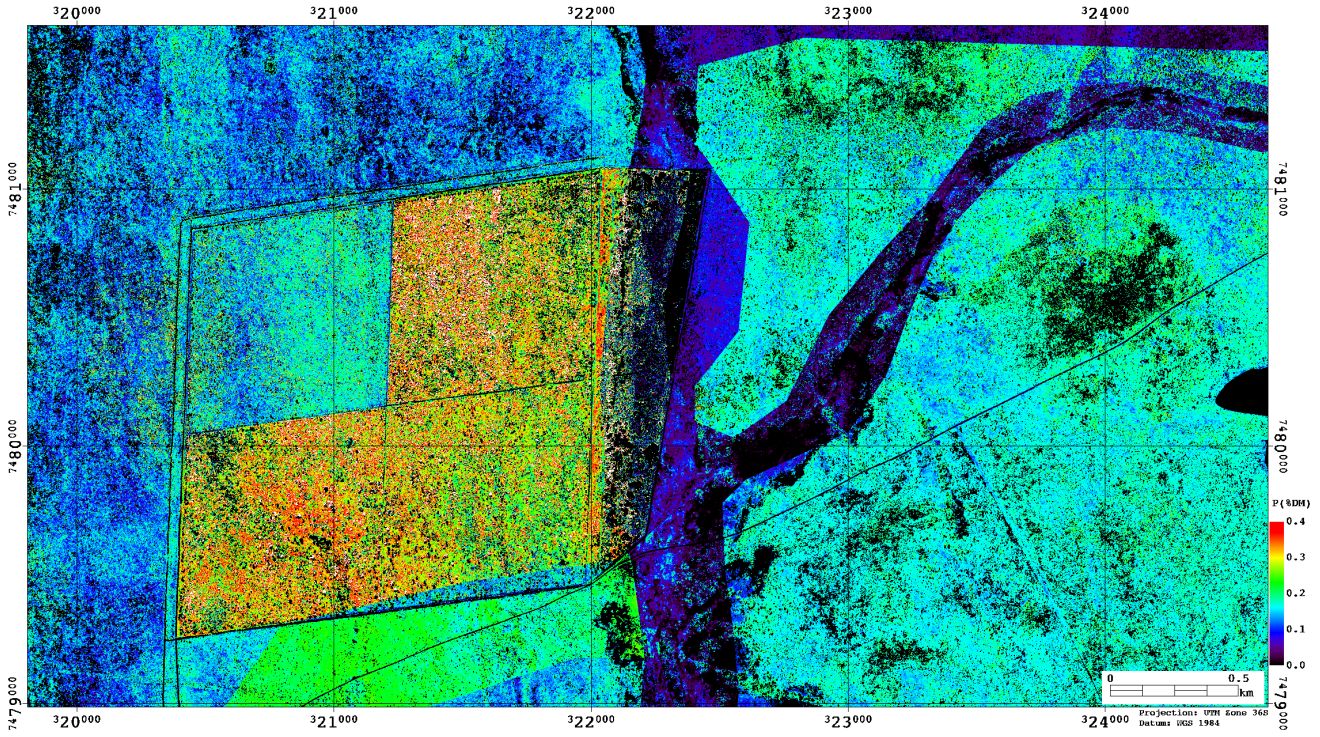
The validation of the inverted models is presented graphically in figure 6.5. The nitrogen and phosphorus validation R^2_{adj} results are below those of the model test results (figure 6.5 vs table 6.2). The fibre validation results are slightly higher than those obtained from testing the model. The graphical presentation of the validation provides the opportunity to see if the model predictions are equally accurate across the entire prediction range.

Predicted nitrogen values (figure 6.5a) were overestimated across the measurement range, although the differences between measured and predicted values was less at higher measured values. Many of the predicted phosphorus validation points (figure 6.5b) closely fitted the measured values. The points not following the 1:1 line were below the line. The field data were re-examined, to see if there were any ecological links (e.g. species, aspect, slope, soils) that could be found to explain the under-estimation of phosphorus values, though no clear explanation was found. The spread of fibre (figure 6.5c) was quite close to the 1:1 line, although values were above the 1:1 at low measured values, and below the line at high measured values.



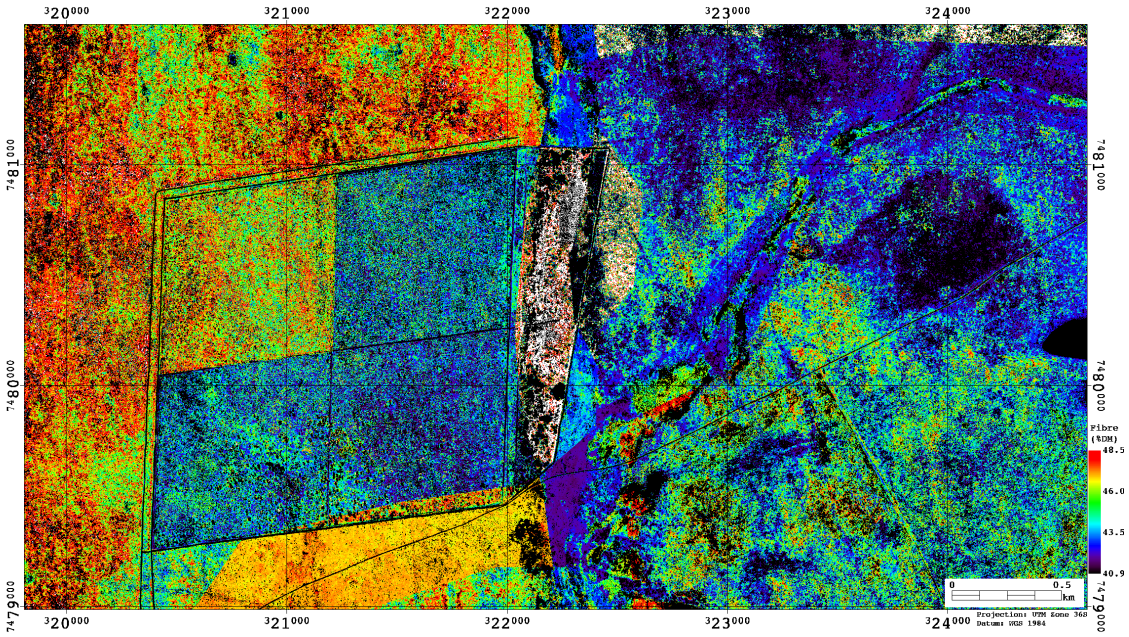
(a) Nitrogen

Figure 6.4: Part 1 of 3: a) Network inversion for nitrogen using the *reduced* model. For further details on this figure please see the later description....



(b) Phosphorus

Figure 6.4: Part 2 of 3: b) Network inversion for phosphorus using the *reduced* data model. For further details on this figure please see the later description ....



(c) Fibre

Figure 6.4: Part 3 of 3: c) Network inversion for fibre using the *reduced* data model.
Dry season nutrient maps generated for the focus study area. Maps were created by inverting the neural network model that was found to minimize the error in prediction, and reduce the cross-track illumination effects present within the CAO Alpha imagery. The network models used to generate the individual figures are marked with an * in table 6.2.

6.5 Discussion

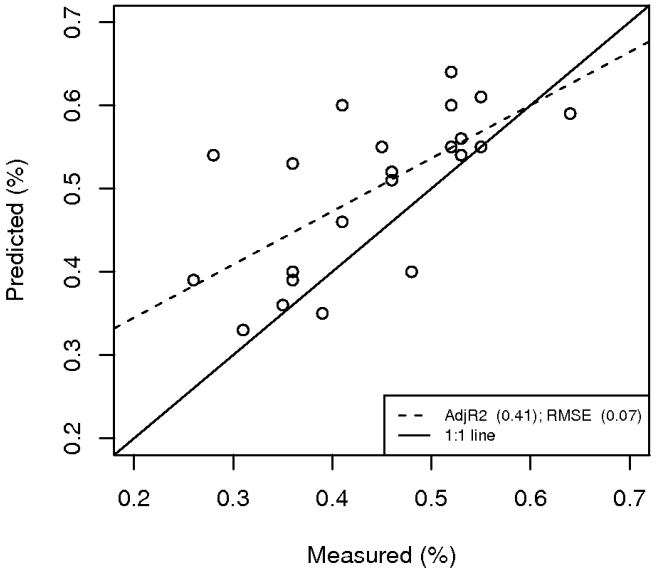
In this study, using CAO Alpha imagery, three forage quality nutrients (nitrogen, phosphorus and fibre) are mapped for the first time, to provide a landscape view of forage quality in a savanna system, during the dry season. In this study an approach of applying a principal component analysis to image data, not only insured that input data for modelling comprised orthogonal layers, but it was a successful means to select components that displayed no cross-track illumination artefacts.

In terms of the application of remote sensing, to the field of nutrient mapping, this study dealt with two pertinent issues: Firstly the state of the vegetation, and secondly the spectral range covered by the sensor. These factors, in combination with considering the ecological considerations of the produced nutrient maps, are discussed for each nutrient. The context of the discussion is based on the impact of mapping the respective forage nutrients.

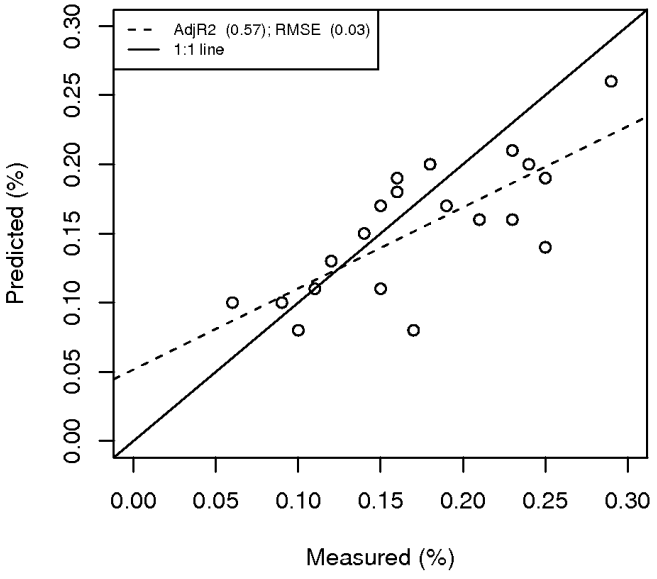
Nitrogen:

Of the three forage nutrients studied here, nitrogen predicted in the dry season had the lowest test and validation precision. Spectroscopic studies that predict nitrogen concentrations in grassland environments, in the wet season, have frequently achieved high accuracies [Albayrak, 2008; Beeri et al., 2007; Mutanga and Skidmore, 2004a; Skidmore et al., 2010]. In an earlier study (see chapter 5), we found that estimation of nitrogen in the dry season was lower than in the wet season. It seems likely that nitrogen will in general be a nutrient that is more difficult to estimate in the dry season.

Over-fitted models, through the inclusion of superfluous data, often results in precise models, that are unable to generalise to new data [Crawley, 2006]. Pre-selection of causal input features, related to a nutrient, may not improve the ability to predict a nutrient, with a given training dataset, however it is expected that such a model can be generalised to new data. Eight features previously linked to nitrogen features, in addition to three ecological variables were used here to predict nitrogen. Although the causal model appeared less affected by over-fitting than the full model (differences between

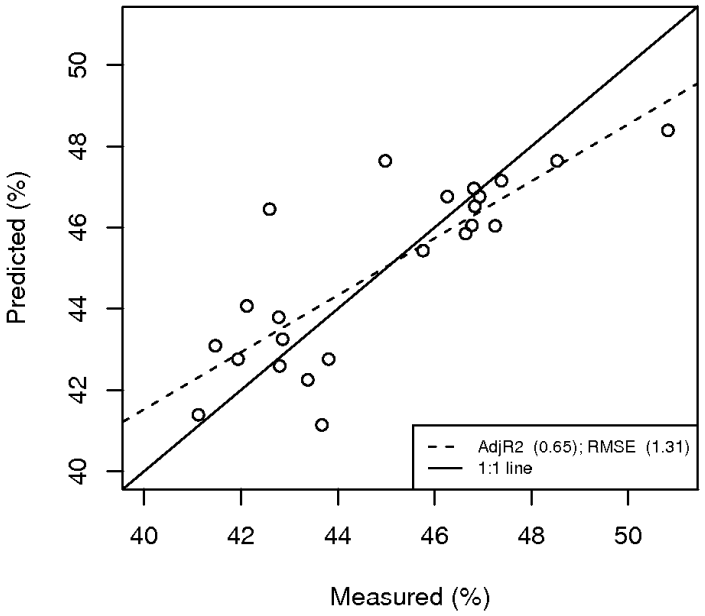


(a) Nitrogen



(b) Phosphorus

Figure 6.5: Part 1 of 2: Validation of the nitrogen and phosphorus nutrient maps (see figure 6.4a and 6.4b), for the detailed figure explanation please see the later description...



(c) Fibre

Figure 6.5: Validation result of the forage nutrient maps (see figure 6.4c). The circles represent the validation points, with the dotted line representing the regression line fit. The results of the fit are presented in the respective legend boxes. The solid 1:1 line is provided as an aid to visualise if the validated points are over or under estimated.

test and training results), contrary to what was expected the causal model was less capable of generalising to a new dataset when compared to the reduced model that did not specifically include causal features (table 6.2).

These findings are not surprising if one considers the physical nature of nitrogen in plants. During the wet season, plant nitrogen is largely associated with photosynthetic pigments and proteins. Photosynthetic pigments primarily reflect within the visible region of the electro-magnetic spectrum [Ustin et al., 2009], and the most prominent of the protein absorption features are located within the SWIR region [Kokaly, 2001; Kokaly et al., 2009]. As plants age, photosynthetic pigments denature, and their contribution to the spectral signal diminishes (chapter 4, figure 4.1). Therefore, in the dry season when most plants have senesced, it would be expected that the visible region of the spectrum would provide a weak contribution

to the estimation of nitrogen concentrations in dry plants. This finding concurs with the findings of Jacquemoud et al. [1995] and Knox et al. [2010], who found that in dry plants the SWIR region contributed the most to nitrogen estimation, and in fresh green plants both the visible and SWIR regions contributed to the discrimination of nitrogen levels in plants. Using only the spectral features of the CAO Alpha imagery for nitrogen detection in the dry season, it would be expected that the closest estimates of nitrogen concentrations would be located in topographical positions associated with increased soil moisture, and therefore vegetation that remains photosynthetic for longer.

The broad patterns associated with nitrogen concentration seen in figure 6.4a appear linked to the soil and fire data included in this analysis. Nitrogen is lowest within the drainage lines, which is in agreement with the finding of Kröger and Rogers [2005]. This was also seen in the images produced in the work of Mutanga and Skidmore [2004a] and Skidmore et al. [2010]. The patterns observed with respect to fire cannot be directly interpreted. The pattern does not indicate that increased fire frequency results in higher nutrient contents, but rather an interaction of fire frequency and intensity. Ideally therefore both fire frequency and fire intensity maps should be included as ancillary input layers. Skidmore et al. [2010] showed a significant positive interaction effect between parent material and fire. In this study all sites were located on a single parent material, but it seems reasonable that if the results of Skidmore et al. [2010] were analysed of the soil type rather than parent material an interaction between soil and fire, similar to what is observed here, would result.

Although it appears that nitrogen levels cannot be directly estimated in the dry season using only spectral features in the VNIR, some variation is captured. The variation is most likely associated with spectral differences associated with different species (also including variations in LAI), and phenological differences associated with micro-topography. Our findings show that nitrogen levels were tied to the ancillary data included in the analysis. If only the VNIR region of a spectrum is available for mapping, we believe that mapping of nitrogen in the dry season would be enhanced through inclusion of mapped ancillary variables, such as species, soil, fire, and phenological maps.

Phosphorus:

When grasses enter senescence, most of the phosphorus within the plant is relocated to the roots [Seastedt, 1988]. Some phosphorus is retained within older leaves and stored as organic phosphorus, this can later be metabolised and moved to younger shoots or leaves for forming key ATP (adenosine triphosphate), nucleic acids and phospholipids [Schachtman et al., 1998].

Similar to the findings of nitrogen, it was seen that the ancillary data had a pronounced impact on the prediction of phosphorus. Fire was shown to play a key role in the predicted concentrations, which is in agreement with the findings of Chambers and Attiwill [1994]; Ferwerda et al. [2006a]. If one interprets the output image obtained in this study, it would appear that phosphorus concentrations are linked to the intensity of fires. The areas that had been burnt on multiple occasions (figure 6.1d) would have had cooler fires in 2004-2005 fire season, and these cooler fires result in lower concentrations of phosphorus over time. This finding is in agreement with Chambers and Attiwill [1994], who found that the availability of nitrogen and phosphorus only increased if fires elevated the soil temperatures between 400–600°C.

Grant and Scholes [2006] reported that by the end of the dry season, on the northern basalts the concentration of phosphorus was below maintenance requirements (0.24% for P, [Duncan, 1992]) for herbivores (wild equids). Our findings show that for most of the system observed, this is already the case early in the dry season. In our study area only the section burnt by a single fire in 2004–2005 had phosphorus levels above the maintenance level.

Detection of phosphorus concentrations by spectra has not been studied to the same extent as compounds such as nitrogen, cellulose, and water [Curran, 1989; Fourty et al., 1996; Kokaly and Clark, 1999]. The total concentration of phosphorus in plants is low [Seastedt, 1988]. Features that would be directly linked to phosphorus, would likely be undetectable due to the overlaps from features found in higher concentrations within plants, e.g. water, cellulose, and nitrogen [Kokaly et al., 2009]. Nonetheless, we show that using the VNIR region of the spectrum and ancillary data, 57% of the variance in phosphorus concentrations can be accounted for. In an earlier study (chapter 3) we linked phosphorus to plant sugars (a product of metabolism - for which phosphorus is directly involved in in

the plant [Schachtman et al., 1998]). Our findings show that absorption features selected to predict foliar phosphorus were located in the SWIR regions. Mutanga and Kumar [2007] selected five bands, through a band selection algorithm, two of which fell within the VNIR region (710 nm and 742 nm) and the remainder in the SWIR region. Osborne et al. [2002] used spectroscopy to detect phosphorus deficiencies in plants; they found that a number of wavelengths within the VNIR region (440, 445, 730 and 930 nm) were significant predictors of phosphorus, but also stated that prediction was best done in the early growth stages of a plant. We believe the CAO Alpha imagery would be more effective in predicting phosphorus in the wet season, but if one wants to map phosphorus irrespective of season a full range sensor is required.

Fibre:

In terms of spectral plant reflectance, the dry season should be the best season to assess the quantity of fibre in plants. At this time, cell water content would be negligible and features (that had been hidden by strong water features) associated with lignin and cellulose would become visible [Elvidge, 1990]. Features associated with fibre are all located within the SWIR regions of the spectrum [Fourty et al., 1996], therefore it would not *a-priori* be expected to achieve good prediction results from an image that covers only the VNIR region of the spectrum.

Of the three nutrients analysed, fibre produced the highest prediction accuracy (65%). The output map of fibre (figure 6.4c) shows detailed variations that would be provided by spectral data rather than the emphasis of the ancillary data that is seen with the nitrogen and phosphorus maps (figure 6.4a and 6.4b). As with nitrogen and phosphorus, the frequency of fires creates a clear pattern in the fibre values. The area with the highest fibre values had been burnt twice, with the last burn in 2004–2005. The remaining area had been burnt either three times or once. The area burnt once was also last burnt in 2004–2005, leaving the question why the fibre values differ between the sites. Similar to our hypothesis that intensity of fire is important for determining phosphorus levels, we believe a similar hypothesis would be appropriate for fibre. The intensity of a fire would be a result of the input fuel load [Elmore et al., 2005]. Therefore in the 2004–2005 fires, the area burnt twice would have had a lower intensity fire, than the area burnt

only once. The time since the last fire, in combination with the intensity of the fire appear to influence fibre concentration (as time since the last fire increases so will fibre concentration, and lower intensity fires result in higher fibre concentrations).

Variations in time since the last fire and fire intensity lead to variations in current standing biomass. In remote sensing, the biomass cover of vegetation (photosynthetic and non-photosynthetic) contributes to the spectral signal of a pixel [Asner, 2004]. Therefore, a pixel covered by a dense layer of grass (and litter) would in total have a stronger signal than a pixel containing less dry litter and only non-photosynthetic vegetation. This leads to the question of whether fibre has in fact been measured or biomass. There was no correlation between the measured fibre values and LAI (used as a measure of biomass -Asner [2004]), further indicating that the output image values explain fibre concentrations found in the field.

Studies by van de Vijver et al. [1999] showed that the effect of post-fire regrowth on plant nutrients was lost by the end of the growing season following a burn. For all nutrients studied here, we observed longer term effects of fires on nutrient concentrations within plants. We propose that this effect does not contradict the findings of van de Vijver et al. [1999], but that it is rather a result of the variable contribution of standing biomass to the signal observed within a pixel, contributing to variances in nutrient levels. It should be tested whether these apparent post-fire related nutrient variations would be evident if calculations are made on a $g.m^{-2}$ rather than the current $g.g^{-1}$.

6.6 Conclusion

In this study our main findings are:

1. The spectral range of the CAO Alpha sensor could be used for mapping nutrients in the dry season, however, results from other field studies show higher precision, with the inclusion of SWIR region information. Therefore if highly precise measurements are required then a complete spectral range sensor would be required.

2. Neural networks effectively generate forage quality maps for savanna grasses in the dry season.

3. Our findings confirmed that ancillary data contributed to mapping of nutrients [Mutanga and Skidmore, 2004a].

4. Reduction of a spectral range through principal components analysis produced results comparable to using an entire spectral range input [Uno et al., 2005], while also reducing model over-fitting.

5. Prior selection of bands known to be linked to a nutrient of interest (*causal input dataset*) did not improve model performance, rather model performance is enhanced through reduction of the entire input dataset using a technique such as principal components analysis.

6. Fire, measured as either intensity or frequency, appears to impact on forage nutrient levels when mapped on a $g.g^{-1}$ basis.

Acknowledgements

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Chapter 7

Mapping forage quality, what's new?

The movement and presence of herbivores in savanna systems, has been attributed to spatial and temporal variations in forage quality [McNaughton, 1990; Fryxell, 2008; Owen-Smith, 2008; Prins and van Langevelde, 2008a]. To capture (and monitor) nutrient variations at landscape scales would provide input for managers and modelers of rangeland and savanna systems. In this thesis, the objective was to determine whether, with the aid of remote sensing (and in particular spectroscopy), both the temporal and spatial variability in savanna forage (grazing) quality could be captured.

An approach was taken which combined spectroscopy and ecology to develop a temporally robust method for mapping forage nutrient concentrations within a savanna system. To capture the temporal aspect of nutrient variation in forage quality models, it was considered pertinent to examine the effects of phenological changes in plants. Phenological changes within plants have been linked to fluctuations in plant nutrients [Jones and Wilson, 1987; McNaughton, 1988; Prins and Beekman, 1989]. Plant phenology also results in changes to reflectance within the electro-magnetic spectrum [Asner, 1998; Dennison and Roberts, 2003; Elvidge, 1990; Irisarri et al., 2009; Kokaly et al., 2009]. Given phenology has ecological implications in nutrient variations and it results in spectroscopic variations, we considered understanding its contribution would provide a relevant step towards developing a method for spatially monitoring nutrients with imaging spectroscopy.

In this synthesis, first the spectroscopic findings that are associated with observed phenological changes in forage nutrient concentrations are highlighted. These findings are the result of a greenhouse study conducted at Wageningen University, The Netherlands. Findings from the greenhouse level were then upscaled to field level, in KNP (RSA), where ecological variables, specific to the field site, were factored into the models. Through this process, models were created that accounted for not only temporal, but also spatial variations in nutrient levels. The field level was then upscaled to airborne spectroscopy to provide a landscape level view of nutrient fluctuations in the KNP, RSA. These three levels are individually considered in terms of the spectroscopic implications for nutrient mapping, and finally brought together to provide an overview on what has been achieved, and what I believe still needs to be considered in the field of nutrient mapping in savanna systems.

Kokaly et al. [2009] recently wrote a comprehensive review about describing and modelling canopy biochemistry from imaging spectroscopy. The review

highlights numerous findings and caveats to the application of biochemical determination. I compare and address my findings, when appropriate, within the scope of this review article.

7.1 Greenhouse level

One of the challenges to the use of imaging spectrometry for biochemical characterisation of vegetation, has been scaling of findings from laboratory → leaf → canopy → landscape levels [Kokaly et al., 2009]. Figure 7.1 schematically outlines how plant reflectance spectral signatures alter with scaling, from laboratory (dried ground material) through to canopy measurements. The alterations are as a result of additional plant properties (e.g. cell contents, cell and leaf structure, etc.), interacting with incoming solar radiation, and finally the reflected illumination is captured as a spectral signal. Figure 7.2 expands on this schema and outlines the scaling of canopy vegetation signatures through to remotely sensed observations of landscapes. The additional factors that contribute to an image's output are highlighted.

The upscaled changes to the spectral signal result in diagnostic features being masked by dominant absorption features (compounds with higher concentrations within the plant) [Kokaly et al., 2009]. Leaf water spectral effects provide a clear example, where an increase in water results in decreased reflectance in the SWIR region, and a feature such as the protein feature at 1420 nm being masked by the water features at 1400 nm and 1450 nm (chapter 2, figure 2.1). In chapter 2, absorption features selected on dried material (≈ laboratory scale) vs fresh material (≈ canopy scale) differed. These findings highlight not only the effects of scaling on spectrum alterations (discussed in depth in Kokaly et al. [2009]), but also the practice of comparing findings between studies made on different plant material states.

A finding independent of the scale of plant measurement (e.g. laboratory or canopy), was that absorption features selected by the stepwise multiple linear regression (sMLR) differed with plant age. These differences might have been as a result of the sMLR method used for analysis, which has received considerable critique [Crawley, 2006; Grossman et al., 1996; Kokaly et al., 2009; Kumar et al., 2001], or as a result of different absorption

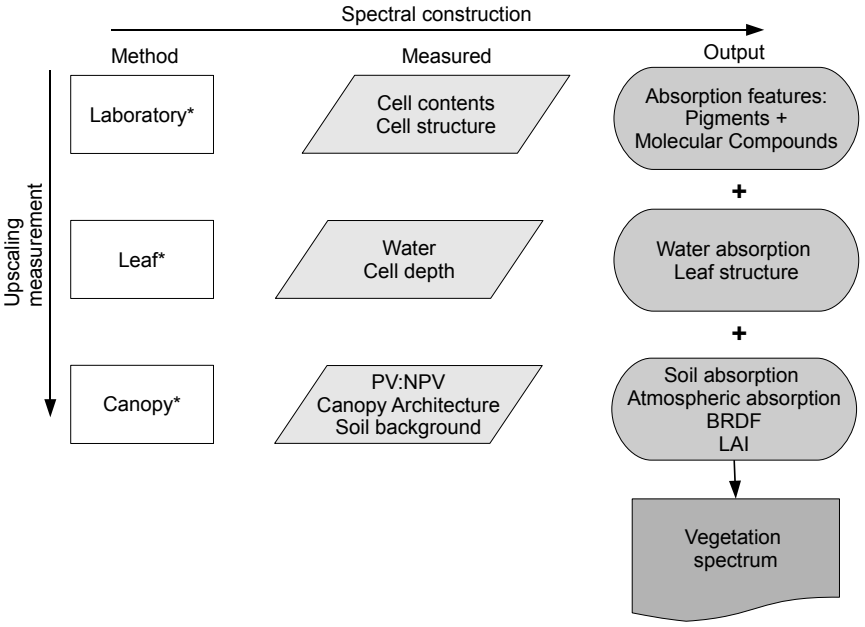

Figure 7.1: Schematic representation of upscaling vegetation spectral measurements from laboratory through to canopy levels.
* Laboratory spectra are taken on dried-ground material, and leaf and canopy spectra are taken on fresh material.

features developing with plant age.

In chapter 3, through an approach of increasing repetitions, re-ordering of input variables, performing forward/backward steps in the sMLR modelling, and comparing findings to partial least squares regression (PLSR), it was possible to critically review the spectral effect of plant ageing on forage quality estimation. Absorption features within the SWIR region from 2180–2380 nm contributed the highest loadings for the three forage nutrients (chapter 3, figure 3.3). The SWIR region has frequently been attributed to containing spectral information related to non-pigment chemicals (e.g. starch, cellulose and proteins) [Jacquemoud et al., 1995; Kokaly, 2001; Mutanga and Kumar, 2007; Nagler et al., 2003]. In the review made by Kokaly et al. [2009], they highlight the need to understand the implications of overlapping absorption features and the spectral relationships

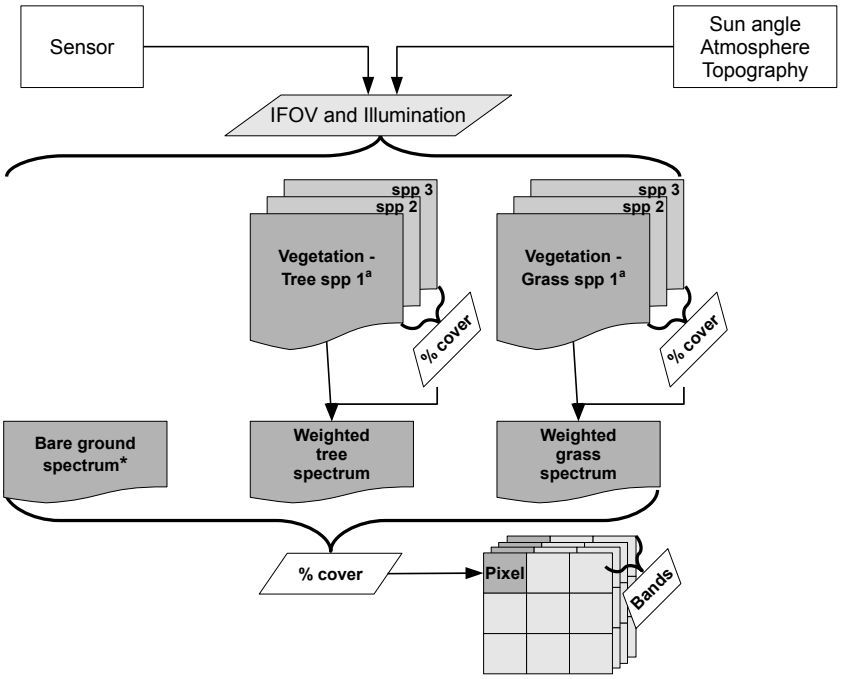

Figure 7.2: Schematic outline of the technical and spectroscopic components that contribute towards a spectral signal obtained in an image pixel.
* for the derivation of the bare ground spectrum (see figure B.1 in appendix B).
[a] the derivation of each vegetation spectrum would follow the physical principles outlined in figure 7.1.

between biochemicals.

The findings of chapter 3 showed that, the relationships between biochemicals and overlapping absorption features were tied to physiological condition of plants. Besides the high loadings in the SWIR region above 2180 nm, in the PLSR models, there were high loadings in spectral regions associated with plant pigments (550, 660–720 nm) and leaf water content (1440, 1940 nm). The inclusion of these spectral features in PLSR was tied to plant physiological condition. The use of sMLR modelling showed how a plants physiology influenced the selection of variables in models. Nitrogen and phosphorus models showed the strongest support for this (chapter 3, table 3.5), where without the inclusion of a plant age co-variant, in the

modelling process, variables were selected across the spectrum, particularly notable was the inclusion of selected wavelengths in close proximity to pigment (430 nm), and water features (990, 1450, 1940 nm), i.e. features that would model plant physiological state. When the plant age co-variant is added to the sMLR modelling process, the only absorption features remaining in the models are those in the SWIR spectral region above 2180 nm.

The presence of a plant biochemical spectral feature can be used to express an ecosystem characteristic. For example, nitrogen features have been used to characterize net primary production [Ollinger et al., 2002], or lignin and cellulose features have quantified leaf litter, which has then been used to investigate nutrient cycling [Wessman et al., 1988; Peterson and Hubbard, 1992]. Results in chapters 2 and 3 showed that physiological condition contributed to nutrient variations. Within the laboratory setting the physiological state was known and controlled for, but in a field setting this information could ideally be derived from imagery. In chapter 4, different indices that could be used to characterize the physiological condition of plants, through remote sensing were investigated. Ageing of a plant was found to be expressed by the depth of the cellulose feature at 2100 nm (Cellulose absorption index [Nagler et al., 2003]), or by an index which combined the area of the VNIR (500–800 nm) and SWIR 2 (2000–2200 nm) features (phenological index (PhIX) - chapter 4). These two areas combined in the PhIX, include the Chl a+b (640, 660 nm), REP (710–730 nm), lignocellulose (2100 nm) and protein (2050, 2180 nm) absorption features, all of which have been associated with ageing of plants (chapter 4).

The contributions of the greenhouse-laboratory experiment, towards the goal of spatially monitoring nutrients in a savanna system, are listed below:

1. Plant biochemical absorption features are unstable, when scaling from laboratory to canopy/field levels. When developing the mapping technique, selection of appropriate features for biochemical estimation should come from canopy level measurements.

2. A plants physiological state, when not considered in conjunction with absorption feature selection, will influence the absorption features selected. In mapping forage nutrients in a savanna environment, where plant physiological conditions will vary across the landscape, ideally plant physiological state should be considered in the nutrient models.

3. PLSR, as a method for model building, captures information for a site that relates not only to specific nutrients, but also accounts for variations in the plant or site. If nutrient models are built from a broad range of sites that capture much of the ecosystem variation (temporal and spatial), then a PLS model would be a suitable means to generalise to multiple sites, as done by Martin et al. [2008] in forest stands. sMLR models are simpler and easier to interpret. If developed carefully, these should provide effective models for mapping. sMLR models, when developed with relevant ancillary data, are shown to provide models of similar predictive capabilities to PLSR models.

4. Derivation of the physiological state of plants through spectroscopy provides an ancillary data layer that can either be used to aid the ecological interpretation of nutrient maps, or be combined to build ecologically variableized sMLR nutrient models.

7.2 Field level

Laboratory level studies revealed, that the physiological state of plant material influenced the prominence of absorption features, for each nutrient. Therefore, as a plant aged different absorption features would gain prominence, therefore in terms of nutrient modelling no features remain consistently significant as plants age (chapter 2 and 3). In upscaling to field level, further variables need to be considered, e.g. species, fire, etc. (chapter 1, figure 1.1). Reviews of forest species have shown that species have their own unique chemical signatures [Asner and Martin, 2009]. Savanna grass species are known to differ in their nutrient contents [Jones and Wilson, 1987; van Oudtshoorn, 1992; Prins and Beekman, 1989], therefore it is likely that these grasses, analysed spectroscopically, would show unique chemical signatures.

At the field level, grass species and soil type were shown to be variables that consistently (temporally) explained variation in the three forage nutrients considered (chapter 5, table 5.4). Conversely, absorption features associated with each of the nutrients altered between seasons (chapter 5, table 5.5). For development of generalised forage nutrient models based on nutrient absorption features alone, the field study highlights that such an approach is challenging in savanna environments. An approach, however,

that builds models with species and soil maps as a base, has the potential to be more accurate. Whether models are built using ecological variables (e.g. soil, species, topography) alone, or by combining spectral absorption features (i.e. features physically linked to a nutrient in question) and ecological variables, it is clear that, per nutrient, a simple linear model approach will not explain the temporal variations in nutrient concentrations within a savanna system (chapter 5, table 5.6). It would be necessary to examine other modelling approaches (e.g. non-linear, Bayesian or decision tree modelling) to capture the spectral changes that occur as a result of seasonal change.

The field level study revealed two additional findings with respect to determining nitrogen concentrations, upscaling, and absorption feature stability. In chapter 2 it was concluded that absorption features derived from dried ground material did not upscale to fresh material, this is logical if one considers that additional components (e.g. water, cell depth and soil background) are captured by the spectrum as one upscales to canopy level (figure 7.1). In the field level spectra taken in the dry season, three of the nitrogen absorption features (1020, 2060, 2130 nm) that were selected when modelling dried ground material (chapter 2, tables 2.3 and 2.5) were again selected when building models using the dry season field spectra (chapter 5, table 5.5). It appears that these absorption features are less affected by leaf structure and canopy architecture, but are rather affected by water content and the quantity of photosynthetic material in the samples.

With respect to canopy measurements of photosynthetic vegetation (taken in the wet season), nitrogen absorption features (the highest contributors to the various principal components) selected in the sMLR modelling were also present in the laboratory sMLR models. This finding is important in terms of nitrogen modelling, as it shows that the absorption features at 640, 910, and 1020 nm are insensitive to the heterogeneity of the savanna grasslands (chapter 2, Tables 2.4, 2.6 and chapter 5, table 5.5).

7.3 Airborne level

Earlier studies that mapped forage related nutrients (nitrogen, phosphorus and tannins) in a savanna system, were performed using hyperspectral imagery obtained during the wet season [Ferwerda, 2005; Mutanga and

Skidmore, 2004a; Mutanga and Kumar, 2007; Skidmore et al., 2010]. The findings in this study showed that seasonal changes (chapter 5) and vegetation physiological condition (chapters 2 and 3) were influential with respect to estimating forage nutrients with hyperspectral data. Findings from the field level showed that combining ecological and spectral information into models would allow for nutrients to be mapped in any season. Creating forage nutrients maps from hyperspectral imagery, deficient in the SWIR spectral region, acquired during the dry season, was an important addition to spectroscopic science. It provided validation for the potential of imaging spectroscopy for mapping nutrient concentrations irrespective of temporal factors (chapter 6). It also highlighted the superiority of imagery for nutrient mapping, that include not only the VNIR region, but also the SWIR region of the spectrum.

In terms of the findings presented in this study, a modelling approach that combines ecological and spectral information into nutrient models, was verified at airborne level. Testing the rigour of this approach at airborne level, where additional spectral and spatial variables would further influence the ability to retrieve biochemical variables from the data (figure 7.2), was an important contribution to support the overall findings. For the first time, it was shown that it is possible to map forage quality (expressed as a combination of three different nutrients), irrespective of season in a savanna system.

In the laboratory and field level, using linear modelling, the SWIR region of the spectrum was shown to contain information relating to the biochemical content of vegetation. These findings were supported by authors that have estimated biochemical variables in vegetation [e.g. Jacquemoud et al., 1995; Kokaly, 2001; Mutanga and Kumar, 2007; Yoder and Pettigrew-Crosby, 1995]. This region of the spectrum was unavailable in the CAO Alpha imagery. Yet, in this study using a non-linear modelling method, validated results (chapter 6, table 6.2) for each nutrient were comparable, but slightly inferior, to the results obtained using the full spectral range on field data (chapter 5, table 5.6). This leads to the question whether, within the VNIR region, nutrient specific spectral features exist that were not considered in this study. Or whether, in this study and earlier biochemical studies, we as spectroscopists, have failed to investigate and consider the non-linear nature of plant biochemicals interactions with light.

7.4 The steps made...

7.4.1 Remote Sensing

In the field of spectroscopic science, for biochemical characterisation of vegetation, in general and specific to savanna regions, this study provided the following insights:

1. Dry season canopy vegetation, and dried-ground vegetation, share absorption features for nitrogen detection. These features are no longer discerned when vegetation is green and fresh. This indicates that overlaps in water and pigment absorption features, rather than leaf and canopy structure, apparently influence detection of nitrogen (and likely other non-pigment biochemicals) (chapter 2).

2. The cellulose feature at 2100 nm, or a combination of biochemically related absorption features (Chl a+b, REP, protein and ligno-cellulose) can be used to explain phenological properties of grasses (chapters 3 and 4).

3. The low concentration of phosphorus in plants, and the lack of absorption features directly linked to this nutrient, challenge repeatable estimation of phosphorus concentrations in plants. With the use of spectral features associated with sugar and starch (as metabolic products), a maximum of 50% of the variation in phosphorus concentrations could be explained (chapters 3, 4 and 5).

4. Ecosystem variables that can be presented spatially provide valuable variables for biochemical model building or model interpretation (chapters 3, 5 and 6).

5. Within heterogeneous savannas, combining ecological variables and spectral absorption features into models, provide statistically significant variables for forage quality modelling (chapters 5 and 6).

6. Forage quality modelling using imaging spectrometry data, can be conducted in both wet and dry seasons. However, variables used for modelling differ between seasons (chapter 5).

7.4.2 Ecology

It has been stated that remote sensing products can make a contribution to the field of ecology, particularly to the field of spatial ecology [Asner and Martin, 2009; Curran, 2001; Kerr and Ostrovsky, 2003; Prins and van Langevelde, 2008b; Ustin, 2004]. This study highlights how ecological findings can contribute to remote sensing, not only in interpretation, but also in development of models. The fusion of ecological and remote sensing knowledge provides a platform from which remote sensing products can be created for use in ecological studies. Plant species and soil type were found to be the two ecological variables that, irrespective of season, significantly contributed to explaining spatial variations in forage nutrient levels. In addition to these two base variables, it was found that seasonally, additional ecological variables (e.g. phenology and fire) significantly contributed to the spatial variation of the forage nutrients (chapter 5).

Contributions of ecology to remote sensing, and remote sensing to ecology, have been the result of the approach taken in this study. The remote sensing products derived, i.e. methods for deriving phenological and forage quality maps, can be implemented into ecological studies such as modelling animal movement and forage selection [Ebrahimi et al., 2010; Pretorius, 2009; Prins and van Langevelde, 2008a; Treydte et al., 2009], to create continuous landscape models, rather than point based models.

7.5 Filling gaps...

This study focuses on individual ecological variables and spectroscopic variables, which when combined create the opportunity to map forage quality in the wet or dry season in savanna's. To achieve repeatable models it is my belief that work still needs to be done on a number of these individual variables. The issues, highlighted in the following paragraphs, would I believe be valuable contributions to characterising biochemical concentrations, not only to spectroscopic science, but ultimately for ecological science.

The ageing of plants was the ecological variable initially considered necessary to capture the temporal variations in forage nutrients detected by imaging spectroscopy (chapter 1). Ecological science (depicted in chapter 1, figure 1.1) has shown that this is the only variable to affect seasonal and

temporal nutrient variations in savanna systems. In this study we showed that within the savanna system, both grass species and soil type (chapter 5) were two ecological variables that signigicantly contributed to explaining nutrient variations. To further continue the approach of combining ecological and spectroscopic findings to model nutrient variations, it needs to be investigated whether these two variables can be reliably classified in spectroscopic terms.

With each addition of individually derived variables in biochemical models, comes the need to evaluate correlation and overlap between variables. Grass species within savanna ecosystems are known to vary in nutrient levels, thereby creating the observed variations in use of different species by herbivores [van Oudtshoorn, 1992; Prins, 1996]. It is thus likely that when deriving a grass species map for a savanna region, elements of the canopy biochemistry would be included. Derived variables (e.g. plant age and species) are likely to contain spectral information from the same regions, as chemicals being derived. For example, in deriving species maps from imaging data, Asner and Vitousek [2005]; Kokaly et al. [2003] and Townsend et al. [2007] all used nutrient absorption properties to separate out species. When combining these variables in nutrient models the implications of possible circularity need to be considered and evaluated.

Both phenological indices (CAI and PhIX) were able to chronologically differentiate the age of grasses. From the greenhouse study, classes were defined with respect to each age group. Testing these on a broader range of plant species and soil types, would identify strengths and limitations of these phenological indices. These phenological indices create continuous values, that should in essence differentiate the ratio of photosynthetic to non-photosynthetic (PV:NPV) within plant spectra. In creating biochemical models based either on physical remote sensing variables (figure 7.1), or based upon ecological variables (chapter 1, figure 1.1), such an index would be a valuable input variable for modelling.

The forage quality maps derived in this study, have been presented in $g.m^{-2}$. From an ecological perspective the quality and quantity of forage is necessary to determine resource sufficiency for different ungulates (e.g. quantity of nutrients required differs for a buffalo, compared to a wildebeest) [Ebrahimi et al., 2010; Prins and Beekman, 1989; Treydte et al., 2009]. In this study the focus has been purely to analyse forage quality, and thus the quantity of the vegetation was not measured. To derive a remote sens-

ing application for forage assessment, that can be used by ecologists, the quantity of vegetation also needs to be determined.

Using remote sensing methods, vegetation biomass (quantity) has been derived. The estimation of biomass, has been extensively applied to green vegetation canopies until they reach full growth. At high biomass concentrations it has been found that the commonly applied NDVI algorithm saturated. Mutanga and Skidmore [2004b], found that with the use of narrow band vegetation indices biomass saturation could be avoided. In ecological studies, the estimation of forage quality is particularly important in the dry season, when animals are most often affected by limited resources. Thus, in terms of forage quality evaluation, it is necessary that plant biomass can be determined in the dry season. An index for estimating biomass therefore needs to be able to perform when plants have entered dormancy, and should be sensitive to capture variations in PV:NPV ratios.

Three separate empirical approaches (PLS, sMLR and ANN) for modelling forage quality, were applied in this work. Of these three approaches, sMLR derived models can be easily interpreted, however, they are limited by the variables used for model building. In Asner [1998, 2004], the non-linear optical properties across the spectrum of the PV:NPV relationship was emphasized. In savanna systems, the vegetation is a gradient of PV:NPV values, and thus with modelling the vegetation within this system, non-linearity in spectral variation will be present. As a result of the hidden layers within neural network models, these non-linear models are difficult to interpret. Yet, they repeatedly produce models with high predictive capabilities on datasets that have been used to construct the model. It appears that modelling of forage nutrients should ideally contain non-linear components. In order to be able to generalise biochemical models between sites and seasons, there needs to be a means to interpret the non-linear features within the models, and in this regard there needs to be further studies.

The suggestions presented above, for future research into the field of spectroscopy for biochemical detection in vegetation, infer that there are still numerous aspects to the field that are unknown. In this work, an insight into the contribution of phenological and seasonal changes to alterations in spectral properties, associated with biochemical constituents in vegetation, has been provided. Mapping of forage quality in dry and wet seasons has been shown to be possible, but it will be through ongoing perseverance of

scientists, ideally in collaboration from different fields, that the application of imaging spectroscopy for continuous monitoring of forage quality in savanna, grassland, and pasture systems will be achieved.

Appendix A

Full vs reduced spectrum empirical methods in biophysical modeling

The analysis of continuous biophysical variables has been performed using different techniques available in spectroscopy. The development of hyperspectral sensors opened up the possibility to perform a range of new investigations that allowed for analysis of detailed physical properties of plants. It also created a problem of having to deal with superfluous data (the "Curse of Dimensionality" [Scott, 1992]). Different statistical techniques have been applied to deal with the superfluous data.

Empirical imaging spectroscopy approaches to nutrient mapping, have either looked at reducing a full range spectrum down to a few selected wavelengths before prediction of nutrients, or used a full spectrum approach using all information available within a spectrum. Some of the methods that have been applied to reduce the dimensionality of hyperspectral data prior to model fitting include, modified stepwise regression [Kokaly and Clark, 1999; Darvishzadeh et al., 2008b; Kawamura et al., 2008], genetic algorithms [Vaiphasa et al., 2007], bootstrap selection [Ferwerda et al., 2006b], wavelet decomposition [Blackburn, 2007; Hsu, 2007], outlier analysis [Chen et al., 2007], and selection based on known physically linked absorption features [Mutanga and Skidmore, 2004a]. The wavelengths selected through

the reduction process are then used as input into developing either linear (multiple linear regression - MLR [Ferwerda et al., 2006b; Chen et al., 2007; Hsu, 2007; Vaiphasa et al., 2007]) or non-linear (Artificial neural networks - ANN [Mutanga and Skidmore, 2004a; Chen et al., 2007]) models.

Both MLR and ANN have been applied in the studies mentioned above and in other studies, but several limitations have been highlighted with both methods. Kumar et al. [2001] summarised the limitations of MLR that have been expressed by numerous authors. ANN overcomes some of these, but the application of non-linear models inherently requires large training sample sizes which are generally unavailable in such studies. An ANN model also requires the use of hidden layers, making the models difficult to interpret, invert and apply to new datasets.

Multicollinearity and overfitting are two of the major drawbacks of the MLR approach. Principal component regression (PCR) and partial least squares regression (PLSR) are two full spectrum methods that have been proposed to overcome these MLR limitations [Geladi and Kowalski, 1986]. In both PCR and PLSR the spectral dataset is collapsed into a small number of vectors. In calculating the vectors, independence between vectors is guaranteed and multicollinearity is thereby avoided. The means of collapsing hyperspectral cubes differs for both methods.

In PCR, only the hyperspectral data matrix is collapsed. If there is large scale variability related to spectral issues, such as brightness or water features, these would be expressed in the first vectors. The risk being, that subtle features, attributed to nutrient fluctuations, would only be extracted in lesser components. In PLSR, collapsing the spectral cube into vectors is done in combination with dependent nutrients. The dependent (nutrient to be predicted) and independent (spectral cube) matrices are related to one another in calculating each vector. A vector is the product of maximum covariance described between the dependent and independent variables [Geladi and Kowalski, 1986; Takahashi et al., 2000]. Vectors produced by PLSR, unlike in PCR, are integrally related to properties of the nutrient of interest.

These full spectrum methods (particularly PLSR) have proven to be reliable and effective for prediction of various nutrients, at single sites, in various biomes e.g., forests [Smith et al., 2002; Huang et al., 2004; Ollinger and Smith, 2005; Asner and Martin, 2008], and grasslands, meadows or

rice fields [Takahashi et al., 2000; Starks et al., 2004; Schut et al., 2005; Darvishzadeh et al., 2008b; Kawamura et al., 2008; Suzuki et al., 2008]. Martin et al. [2008] has shown that a calibration model developed, using PLSR, at one site could be applied to multiple forest stands.

Appendix B

Construction of bare ground spectra

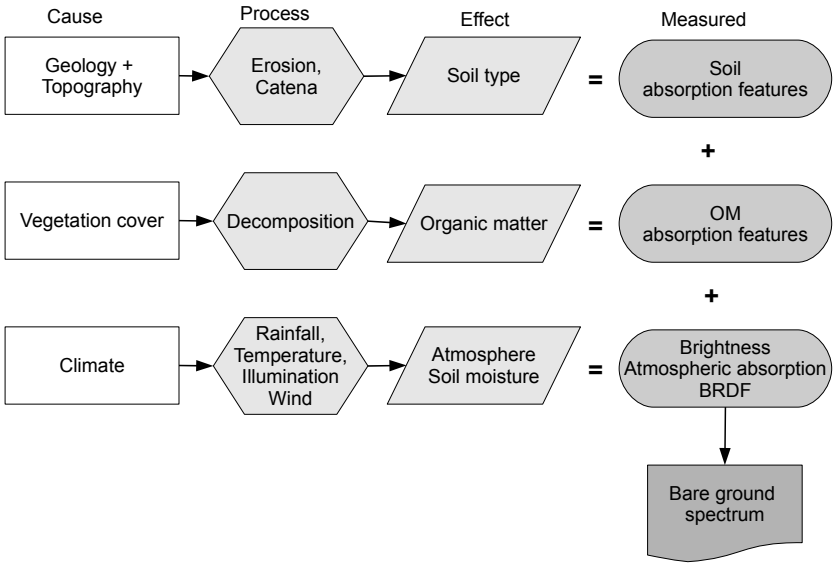

Figure B.1: Ecological parameters, and the processes and how they contribute to a measured bare ground/soil spectrum.

Bibliography

Albayrak, S. (2008). Use of reflectance measurements for the detection of N, P, K, ADF and NDF contents in Sainfoin pasture. *Sensors*, 8(11):7275–7286.

Allred, B. and Snyder, K. (2008). Ecophysiological responses of Chihuahuan desert grasses to fire. *Journal of Arid Environments*, 72(11):1989–1996.

AOAC (1970). *Official Method of Analysis*. Association of Official Analytical Chemists, Washington DC, 11th edition.

Archibald, S. (2008). African grazing lawns - how fire, rainfall, and grazer numbers interact to affect grass community states. *Journal of Wildlife Management*, 72(2):492–501.

Archibald, S. and Scholes, R. (2007). Leaf green-up in a semi-arid african savanna - separating tree and grass responses to environmental cues. *Journal of Vegetation Science*, 18(4):583–594.

Asner, G. P. (1998). Biophysical and biochemical sources of variability in canopy reflectance. *Remote Sensing of Environment*, 64:234–253.

Asner, G. P. (2004). *Remote Sensing for Natural Resource Management and Environmental Monitoring*, volume 4 of *Manual of Remote Sensing*, Chapter: Biophysical remote sensing signatures of arid and semiarid ecosystems, pages 53–109. John Wiley & Sons, 3rd edition.

Asner, G. P., Elmore, A. J., Flint Hughes, R., Warner, A. S., and Vitousek, P. M. (2005). Ecosystem structure along bioclimatic gradients in Hawai'i from imaging spectroscopy. *Remote Sensing of Environment*, 96(3-4):497–508.

Asner, G. P. and Heidebrecht, K. B. (2002). Spectral unmixing of vegetation, soil and dry carbon cover in arid regions: comparing multispectral and hyperspectral observations. *International Journal of Remote Sensing*, 23(19):3939–3958.

Asner, G. P., Knapp, D. E., Kennedy-Bowdoin, T., Jones, M. O., Martin, R. E., Boardman, J., and Field, C. B. (2007). Carnegie airborne observatory: in-flight fusion of hyperspectral imaging and waveform light detection and ranging for three-dimensional studies of ecosystems. *Journal of Applied Remote Sensing*, 1:013536–21.

Asner, G. P., Levick, S. R., Kennedy-Bowdoin, T., Knapp, D. E., Emerson, R., Jacobson, J., Colgan, M. S., and Martin, R. E. (2009). Large-scale impacts of

herbivores on the structural diversity of african savannas. *Proceedings of the National Academy of Sciences*, 106(12):4947–4952.

Asner, G. P. and Lobell, D. B. (2000). A biogeophysical approach for automated swir unmixing of soils and vegetation. *Remote Sensing of Environment*, 74(1):99–112.

Asner, G. P. and Martin, R. E. (2008). Spectral and chemical analysis of tropical forests: Scaling from leaf to canopy levels. *Remote Sensing of Environment*, 112(10):3958–3970.

Asner, G. P. and Martin, R. E. (2009). Airborne spectranomics: mapping canopy chemical and taxonomic diversity in tropical forests. *Frontiers in Ecology and the Environment*, 7(5):269–276.

Asner, G. P. and Vitousek, P. M. (2005). Remote analysis of biological invasion and biogeochemical change. *Proceedings of the National Academy of Sciences of the United States of America*, 102(12):4383–4386.

Asner, G. P., Wessman, C. A., Bateson, C. A., and Privette, J. L. (2000). Impact of tissue, canopy, and landscape factors on the hyperspectral reflectance variability of arid ecosystems. *Remote Sensing of Environment*, 74(1):69–84.

Atkinson, P. M. and Tatnall, A. R. L. (1997). Neural networks in remote sensing - introduction. *International Journal Of Remote Sensing*, 18(4):699–709.

Augustine, D. J. (2003). Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an east african savanna. *Journal of Applied Ecology*, 40(1):137–149.

Baret, F. and Guyot, G. (1991). Potentials and limits of vegetation indices for lai and apar assessment. *Remote Sensing of Environment*, 35(2-3):161–173.

Baret, F., Jacquemoud, S., and Hanocq, J. F. (1993). About the soil line concept in remote sensing. *Advances in Space Research*, 13(5):281–284.

Barton II, F. and Windham, W. (1988). Determination of acid-detergent fiber and crude protein in forages by near-infrared reflectance spectroscopy: collaborative study. *Journal Association of Official Analytical Chemists*, 71:620–651.

Beck, P. S. A., Jönsson, P., Hgda, K. A., Karlsen, S. R., Eklundh, L., and Skidmore, A. K. (2007). A ground-validated ndvi dataset for monitoring vegetation dynamics and mapping phenology in Fennoscandia and the Kola peninsula. *International Journal of Remote Sensing*, 28(19):4311–4330.

Beck, P. S. A., Wang, T. J., Skidmore, A. K., and Liu, X. H. (2008). Displaying remotely sensed vegetation dynamics along natural gradients for ecological studies. *International Journal of Remote Sensing*, 29(14):4277–4283.

Beeri, O., Phillips, R., Hendrickson, J., Frank, A. B., and Kronberg, S. (2007). Estimating forage quantity and quality using aerial hyperspectral imagery for northern mixed-grass prairie. *Remote Sensing of Environment*, 110(2):216–225.

Blackburn, G. A. (1998). Quantifying chlorophylls and caroteniods at leaf and canopy scales: An evaluation of some hyperspectral approaches. *Remote Sensing of Environment*, 66(3):273–285.

Blackburn, G. A. (2007). Wavelet decomposition of hyperspectral data: a novel approach to quantifying pigment concentrations in vegetation. *International Journal of Remote Sensing*, 28(12):2831–2855.

Bradley, B. A., Jacob, R. W., Hermance, J. F., and Mustard, J. F. (2007). A curve fitting procedure to derive inter-annual phenologies from time series of noisy satellite NDV data. *Remote Sensing of Environment*, 106(2):137–145.

Bradley, B. A. and Mustard, J. F. (2005). Identifying land cover variability distinct from land cover change: Cheatgrass in the great basin. *Remote Sensing of Environment*, 94(2):204–213.

Butterfield, H. S. and Malmström, C. M. (2009). The effects of phenology on indirect measures of aboveground biomass in annual grasses. *International Journal of Remote Sensing*, 30(12):3133–3146.

Card, D. H., Peterson, D. L., Matson, P. A., and Aber, J. D. (1988). Prediction of leaf chemistry by the use of visible and near infrared reflectance spectroscopy. *Remote Sensing of Environment*, 26(2):123–147.

Chambers, D. and Attiwill, P. (1994). The ash-bed effect in *Eucalyptus regnans* forest: Chemical, physical and microbiological changes in soil after heating or partial sterilisation. *Australian Journal of Botany*, 42(6):739–749.

Chapin III, F. S. (1980). The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, 11(1):233–260.

Chen, L., Huang, J. F., Wang, F. M., and Tang, Y. L. (2007). Comparison between back propagation neural network and regression models for the estimation of pigment content in rice leaves and panicles using hyperspectral data. *International Journal of Remote Sensing*, 28(16):3457–3478.

Cho, M. A. and Skidmore, A. K. (2006). A new technique for extracting the red edge position from hyperspectral data: The linear extrapolation method. *Remote Sensing of Environment*, 101(2):181–193.

Cho, M. A., Skidmore, A. K., Corsi, F., van Wieren, S. E., and Sobhan, I. (2007). Estimation of green grass/herb biomass from airborne hyperspectral imagery using spectral indices and partial least squares regression. *International Journal of Applied Earth Observation and Geoinformation*, 9(4):414–424.

Clark, D. (1989). *Near Infrared Reflectance Spectroscopy (NIRS): Analysis of Forage Quality*, Chapter: History of NIRS analysis of agricultural products, pages 7–11. USDA, Agricultural Research Service.

Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A., and Schwartz, M. D. (2007). Shifting plant phenology in response to global change. *Trends in Ecology & Evolution*, 22(7):357–365.

Craine, J. M., Ballantyne, F., Peel, M., Zambatis, N., Morrow, C., and Stock, W. D. (2009). Grazing and landscape controls on nitrogen availability across 330 south african savanna sites. *Austral Ecology*, 34(7):731–740.

Crawley, M. (2006). *Statistical computing: an introduction to data analysis using S-Plus*. John Wiley & Sons, England.

Curran, P. J., Dungan, J., Macler, B., and Plummer, S. (1992). Reflectance spectroscopy of fresh whole leaves for the estimation of chemical concentration. *Remote Sensing of Environment*, 39:153–166.

Curran, P. J., Kupiec, J., and Smith, G. (1997). Remote sensing the biochemical composition of a slash pine canopy. *IEEE Transactions on Geoscience and Remote Sensing*, 35:415–420.

Curran, P. J. (1989). Remote sensing of foliar chemistry. *Remote Sensing of Environment*, 30(3):271–278.

Curran, P. J. (2001). Imaging spectrometry for ecological applications. *International Journal of Applied Earth Observation and Geoinformation*, 3(4):305–312.

Curran, P. J., Dungan, J. L., and Peterson, D. L. (2001). Estimating the foliar biochemical concentration of leaves with reflectance spectrometry: Testing the kokaly and clark methodologies. *Remote Sensing of Environment*, 76(3):349–359.

Darvishzadeh, R., Skidmore, A. K., Schlerf, M., and Atzberger, C. (2008a). Inversion of a radiative transfer model for estimating vegetation lai and chlorophyll in a heterogeneous grassland. *Remote Sensing of Environment*, 112(5):2592–2604.

Darvishzadeh, R., Skidmore, A. K., Schlerf, M., Atzberger, C., Corsi, F., and Cho, M. A. (2008b). Lai and chlorophyll estimation for a heterogeneous grassland using hyperspectral measurements. *International Journal of Photogrammetry and Remote Sensing*, 63:409–426.

Darvishzadeh, R., Skidmore, A. K., Atzberger, C., and van Wieren, S. E. (2008c). Estimation of vegetation lai from hyperspectral reflectance data: Effects of soil type and plant architecture. *International Journal of Applied Earth Observation and Geoinformation*, 10(3):358–373.

Delbart, N., Kergoat, L., Le Toan, T., Lhermitte, J., and Picard, G. (2005). Determination of phenological dates in boreal regions using normalized difference water index. *Remote Sensing of Environment*, 97(1):26–38.

Delbart, N., Le Toan, T., Kergoat, L., and Fedotova, V. (2006). Remote sensing of spring phenology in boreal regions: A free of snow-effect method using noaa-avhrr and spot-vgt data (1982-2004). *Remote Sensing of Environment*, 101(1):52–62.

Dennison, P. E. and Roberts, D. A. (2003). The effects of vegetation phenology on endmember selection and species mapping in southern california chaparral. *Remote Sensing of Environment*, 87(2-3):295–309.

du Toit, J. (2003). *The Kruger Experience: Ecology and management of savanna heterogeneity*, Chapter: Large herbivores and savanna heterogeneity, pages 292–309. Island Press.

du Toit, J., Rogers, K., and Biggs, H. (2003). *The Kruger Experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.

Duncan, P. B. P. B. (1992). *Horses and grasses : the nutritional ecology of equids and their impact on the Camargue / Patrick Duncan*. Springer-Verlag, New

York :.

Ebrahimi, A., Milotic, T., and Hoffmann, M. (2010). A herbivore specific grazing capacity model accounting for spatio-temporal environmental variation: A tool for a more sustainable nature conservation and rangeland management. *Ecological Modelling*, 221(6):900–910.

Elmore, A. J., Asner, G. P., and Hughes, R. F. (2005). Satellite monitoring of vegetation phenology and fire fuel conditions in hawaiian drylands. *Earth Interactions*, 9(21):1–21.

Elvidge, C. D. (1990). Visible and near infrared reflectance characteristics of dry plant materials. *International Journal Remote Sensing*, 11:1775–1795.

Elvidge, C. D. and Portigal, F. P. (1990). Change detection in vegetation using 1989 AVIRIS data. *SPIE-The International Society for Optical Engineering*, 1298:178–189.

Ferwerda, J. G. (2005). *Charting the Quality of Forage: Measuring and Mapping the Variation of Chemical Components in Foliage with Hyperspectral Remote Sensing*. Phd, International Institute for Geo-information Science and Earth Observation and Wageningen University.

Ferwerda, J. G., Siderius, W., van Wieren, S. E., Grant, C. C, Peel, M., Skidmore, A. K., and Prins, H. H. T. (2006a). Parent material and fire as principle drivers of foliage quality in woody plants. *Forest Ecology and Management*, 231(1-3):178 – 183.

Ferwerda, J. G. and Skidmore, A. K. (2007). Can nutrient status of four woody plant species be predicted using field spectrometry? *ISPRS Journal of Photogrammetry and Remote Sensing*, 62(6):406 – 414.

Ferwerda, J. G., Skidmore, A. K., and Stein, A. (2006b). A bootstrap procedure to select hyperspectral wavebands related to tannin content. *International Journal of Remote Sensing*, 27(7):1413–1424.

Fourty, T., Baret, F., Jacquemoud, S., Schmuck, G., and Verdebout, J. (1996). Leaf optical properties with explicit description of its biochemical composition: Direct and inverse problems. *Remote Sensing of Environment*, 56(2):104–117.

Fryxell, J. M. (2008). *Resource Ecology: Spatial and temporal dynamics of foraging*, Chapter: Predictive modelling of patch used by terrestrial herbivores, pages 105–123. Springer.

Furnival, G. M. and Wilson, Robert W., J. (1974). Regressions by leaps and bounds. *Technometrics*, 16(4):499–511.

Gao, B.-c. (1996). NDWI–a normalized difference water index for remote sensing of vegetation liquid water from space. *Remote Sensing of Environment*, 58(3):257–266.

Garcia, M. and Ustin, S. L. (2001). Detection of interannual vegetation responses to climatic variability using aviris data in a coastal savanna in california. *Geoscience and Remote Sensing, IEEE Transactions on*, 39(7):1480–1490.

Gastellu-Etchegorry, J. P. and Bruniquel-Pinel, V. (2001). A modeling approach to

assess the robustness of spectrometric predictive equations for canopy chemistry. *Remote Sensing of Environment*, 76(1):1–15.

Geladi, P. and Kowalski, B. R. (1986). Partial least-squares regression: a tutorial. *Analytica Chimica Acta*, 185:1–17.

Gertenbach, W. (1983). Landscapes of the kruger national park. *Koedoe*, 26:9–121.

Gianelle, D. and Guastella, F. (2007). Nadir and off-nadir hyperspectral field data: strengths and limitations in estimating grassland biophysical characteristics. *International Journal of Remote Sensing*, 28(7):1547–1560.

Goel, P. K., Prasher, S. O., Landry, J. A., Patel, R. M., Bonnell, R. B., Viau, A. A., and Miller, J. R. (2003). Potential of airborne hyperspectral remote sensing to detect nitrogen deficiency and weed infestation in corn. *Computers and Electronics in Agriculture*, 38(2):99–124.

Grant, C., Peel, M., Zambatis, N., and van Ryssen, J. (2000). Nitrogen and phosphorus concentration in faeces: an indicator of range quality as a practical adjunct to existing range evaluation methods. *African Journal of Range & Forage Science*, 17:81–92.

Grant, C. and Scholes, M. (2006). The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. *Biological Conservation*, 130(3):426–437.

Grant, J., Hopcraft, C., Olff, H., and Sinclair, A. (2010). Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution*, 25(2):119–128.

Grossman, Y. L., Ustin, S. L., Jacquemoud, S., Sanderson, E. W., Schmuck, G., and Verdebout, J. (1996). Critique of stepwise multiple linear regression for the extraction of leaf biochemistry information from leaf reflectance data. *Remote Sensing of Environment*, 56(3):182–193.

Hartshorn, A. S., Coetsee, C., and Chadwick, O. A. (2009). Pyromineralization of soil phosphorus in a south african savanna. *Chemical Geology*, 267(1-2):24–31.

Heitkönig, I. and Owen-Smith, N. (1998). Seasonal selection of soil types and grass swards by roan antelope in a south african savanna. *African Journal of Ecology*, 36(1):57–70.

Himmelsbach, D. (2000). *Forage evaluation in ruminant nutrition*, Chapter: NMR and other physicochemical techniques for forage assessment, pages 321–345. CABI Publishing, Oxon, UK.

Hsu, P.-H. (2007). Feature extraction of hyperspectral images using wavelet and matching pursuit. *ISPRS Journal of Photogrammetry and Remote Sensing*, 62(2):78–92.

Huang, C.-Y. and Geiger, E. L. (2008). Climate anomalies provide opportunities for large-scale mapping of non-native plant abundance in desert grasslands. *Diversity and Distributions*, 14(5):875–884.

Huang, Z., Turner, B. J., Dury, S. J., Wallis, I. R., and Foley, W. J. (2004). Estimating foliage nitrogen concentration from hymap data using continuum

removal analysis. *Remote Sensing of Environment*, 93(1-2):18–29.

Huesca, M., Litago, J., Palacios-Orueta, A., Montes, F., Sebastin-Lpez, A., and Escribano, P. (2009). Assessment of forest fire seasonality using modis fire potential: A time series approach. *Agricultural and Forest Meteorology*, 149(11):1946–1955.

Irisarri, J. G. N., Oesterheld, M., Vern, S. R., and Paruelo, J. M. (2009). Grass species differentiation through canopy hyperspectral reflectance. *International Journal of Remote Sensing*, 30(22):5959–5975.

Jacquemoud, S., Bacour, C., Poilv, H., and Frangi, J. P. (2000). Comparison of four radiative transfer models to simulate plant canopies reflectance: Direct and inverse mode. *Remote Sensing of Environment*, 74(3):471–481.

Jacquemoud, S., Baret, F., and Hanocq, J. (1992). Modeling spectral and bidirectional soil reflectance. *Remote Sensing of Environment*, 41(2-3):123–132.

Jacquemoud, S., Verdebout, J., Schmuck, G., Andreoli, G., and Hosgood, B. (1995). Investigation of leaf biochemistry by statistics. *Remote Sensing of Environment*, 54(3):180–188.

Jacquemoud, S., Verhoef, W., Baret, F., Bacour, C., Zarco-Tejada, P. J., Asner, G. P., Franois, C. and Ustin, S. L. (2009). PROSPECT+SAIL models: A review of use for vegetation characterization. *Remote Sensing of Environment*, 113(Supplement 1):S56–S66.

Johnson, L. F. and Billow, C. R. (1996). Spectrometry estimation of total nitrogen concentration in douglas-fir foliage. *International Journal of Remote Sensing*, 17(3):489–500.

Johnson, L. F., Hlavka, C. A., and Peterson, D. L. (1994). Multivariate analysis of aviris data for canopy biochemical estimation along the oregon transect. *Remote Sensing of Environment*, 47(2):216–230.

Jones, D. and Wilson, A. (1987). *The nutrition of herbivores*, Chapter: Nutritive quality of forage, pages 65–89. Academic Press.

Kathuroju, N., White, M. A., Symanzik, J., Schwartz, M. D., Powell, J. A., and Nemani, R. R. (2007). On the use of the advanced very high resolution radiometer for development of prognostic land surface phenology models. *Ecological Modelling*, 201(2):144–156.

Kawamura, K., Watanabe, N., Sakanoue, S., and Inoue, Y. (2008). Estimating forage biomass and quality in a mixed sown pasture based on partial least squares regression with waveband selection. *Grassland Science*, 54(3):131–145.

Kerr, J. T. and Ostrovsky, M. (2003). From space to species: ecological applications for remote sensing. *Trends in Ecology & Evolution*, 18(6):299–305.

Knox, N. M., Skidmore, A. K., Schlerf, M., de Boer, W. F., van Wieren, S. E., van der Waal, C., Prins, H. H. T., and Slotow, R. (2010). Nitrogen prediction in grasses: Effect of bandwidth and plant material state on absorption feature selection. *International Journal of Remote Sensing*, 31(3):691–704.

Kokaly, R. F. (2001). Investigating a physical basis for spectroscopic estimates of

leaf nitrogen concentration. *Remote Sensing of Environment*, 75(2):153–161.

Kokaly, R. F., Asner, G. P., Ollinger, S. V., Martin, M. E., and Wessman, C. A. (2009). Characterizing canopy biochemistry from imaging spectroscopy and its application to ecosystem studies. *Remote Sensing of Environment*, 113(Supplement 1):S78–S91.

Kokaly, R. F. and Clark, R. N. (1999). Spectroscopic determination of leaf biochemistry using band-depth analysis of absorption features and stepwise multiple linear regression. *Remote Sensing of Environment*, 67(3):267–287.

Kokaly, R. F., Despain, D. G., Clark, R. N., and Livo, K. E. (2003). Mapping vegetation in yellowstone national park using spectral feature analysis of aviris data. *Remote Sensing of Environment*, 84(3):437–456.

Koltunov, A., Ustin, S. L., Asner, G. P., and Fung, I. (2009). Selective logging changes forest phenology in the brazilian amazon: Evidence from modis image time series analysis. *Remote Sensing of Environment*, 113(11):2431–2440.

Kröger, R. and Rogers, K. H. (2005). Roan (*Hippotragus equinus*) population decline in Kruger National Park, South Africa: influence of a wetland boundary. *European Journal of Wildlife Research*, 51(1):25–30.

Kumar, L., Schmidt, K., Dury, S., and Skidmore, A. K. (2001). *Imaging Spectrometry*, Chapter: Imaging spectrometry and vegetation science, pages 111–155. Kluwer Academic Publishers.

Lamb, D. W., Steyn-Ross, M., Schaare, P., Hanna, M. M., Silvester, W., and Steyn-Ross, A. (2002). Estimating leaf nitrogen concentration in ryegrass (*Lolium* spp.) pasture using the chlorophyll red-edge: theoretical modelling and experimental observations. *International Journal of Remote Sensing*, 23(18):3619–3648.

Levick, S. R. and Rogers, K. (2008). Patch and species specific responses of savanna woody vegetation to browser exclusion. *Biological Conservation*, 141(2):489–498.

Levick, S. R., Asner, G. P., Kennedy-Bowdoin, T., and Knapp, D. E. (2009). The relative influence of fire and herbivory on savanna three-dimensional vegetation structure. *Biological Conservation*, 142(8):1693–1700.

Ludwig, F., de Kroon, H., Berendse, F., and Prins, H. H. T. (2004). The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology*, 170(1):93–105.

Macvicar, C., Loxton, R., Lambrechts, J., le Roux, J., de Villiers, J., Verster, E., Merryweather, F., and van Rooyen, T. (1977). Soil classification: a binomial system for south africa. Technical report, Soil and Irrigation Research Institute, Department of Agricultural Technical Services, Division of Agricultural Information, Pvt bag X144, Pretoria, 0001.

Marsett, R. C., Qi, J., Heilman, P., Biedenbender, S. H., Watson, M. C., Amer, S., Weltz, M., Goodrich, D., and Marsett, R. (2006). Remote sensing for grassland management in the arid southwest. *Rangeland Ecology & Management*,

59(5):530–540.

Marten, G., Shenk, J., and Barton II, F. (1989). *Near Infrared Reflectance Spectroscopy (NIRS): Analysis of Forage Quality*. USDA, Agricultural Research Service, USDA, Agricultural Research Service, Washington D.C., agricultural handbook no. 643 edition.

Martin, M. and Aber, J. (1997). High spectral resolution remote sensing of forest canopy lignin, nitrogen and ecosystem processes. *Ecological Applications*, 7:431–443.

Martin, M., Plourde, L., Ollinger, S., Smith, M.-L., and McNeil, B. (2008). A generalizable method for remote sensing of canopy nitrogen across a wide range of forest ecosystems. *Remote Sensing of Environment*, 112(9):3511–3519.

Matson, P., Johnson, L., Billow, C., Miller, J., and Pu, R. (1994). Seasonal patterns and remote spectral estimation of canopy chemistry across the oregon transect. *Ecological Applications*, 4(2):280–298.

McCoy, R. (2005). *Field methods in remote sensing*. Guilford Press, New York etc.

McNaughton, S. J. (1990). Mineral nutrition and seasonal movement of african migratory ungulates. *Nature*, 345:613–615.

McNaughton, S. J. and Banyikwa, F. (1995). Plant communities and herbivory. In Sinclair, A. and Arcese, P., editors, *Serengeti II - dynamics, management, and conservation of an ecosystem*, pages 49–70. Chicago Press, Chicago.

McNaughton, S. J. (1987). *The nutrition of herbivores*, Chapter: Adaptation of herbivores to seasonal changes in nutrient supply, pages 391–408. Academic Press.

McNaughton, S. J. (1988). Mineral nutrition and spatial concentrations of african ungulates. *Nature*, 334(6180):343–345.

Mevik, B.-H. and Cederkvist, H. R. (2004). Mean squared error of prediction (msep) estimates for principal component regression (pcr) and partial least squares regression (plsr). *Journal of Chemometrics*, 18(9):422–429.

Mingo, A. and Oesterheld, M. (2009). Retention of dead leaves by grasses as a defense against herbivores. a test on the palatable grass *Paspalum dilatatum*. *Oikos*, 118(5):753–757.

Mirik, M., Norland, J. E., Crabtree, R. L., and Biondini, M. E. (2005). Hyperspectral one-meter-resolution remote sensing in yellowstone national park, wyoming: I. forage nutritional values. *Rangeland Ecology & Management*, 58(5):452–458.

Monteiro, S. T., Minekawa, Y., Kosugi, Y., Akazawa, T., and Oda, K. (2007). Prediction of sweetness and amino acid content in soybean crops from hyperspectral imagery. *ISPRS Journal of Photogrammetry and Remote Sensing*, 62(1):2–12.

Mutanga, O. (2004). *Hyperspectral Remote Sensing of Tropical Grass Quality and Quantity*. Phd, International Institute for Geo-information Science and Earth Observation and Wageningen University.

Mutanga, O. and Kumar, L. (2007). Estimating and mapping grass phosphorus

concentration in an african savanna using hyperspectral image data. *International Journal of Remote Sensing*, 28(21):4897–4911.

Mutanga, O., Prins, H. H. T., Skidmore, A. K., Wieren, S. E., Huizing, H., Grant, C. C., Peel, M., and Biggs, H. (2004a). Explaining grass-nutrient patterns in a savanna rangeland of southern africa. *Journal of Biogeography*, 31(5):819–829.

Mutanga, O. and Skidmore, A. K. (2004a). Integrating imaging spectroscopy and neural networks to map grass quality in the kruger national park, south africa. *Remote Sensing of Environment*, 90(1):104–115.

Mutanga, O. and Skidmore, A. K. (2004b). Narrow band vegetation indices solve the saturation problems in biomass estimation. *International Journal of Remote Sensing*, 25:1–16.

Mutanga, O. and Skidmore, A. K. (2007). Red edge shift and biochemical content in grass canopies. *ISPRS Journal of Photogrammetry and Remote Sensing*, 62(1):34–42.

Mutanga, O., Skidmore, A. K., and Prins, H. H. T. (2004b). Discriminating sodium concentration in a mixed grass species environment of the kruger national park using field spectrometry. *International Journal of Remote Sensing*, 25(20):4191–4201.

Mutanga, O., Skidmore, A. K., and Prins, H. H. T. (2004c). Predicting in situ pasture quality in the kruger national park, south africa, using continuum-removed absorption features. *Remote Sensing of Environment*, 89(3):393–408.

Mutanga, O., Skidmore, A. K., and van Wieren, S. E. (2003). Discriminating tropical grass (cenchrus ciliaris) canopies grown under different nitrogen treatments using spectroradiometry. *ISPRS Journal of Photogrammetry and Remote Sensing*, 57(4):263–272.

Nagler, P. L., Daughtry, C. S. T., and Goward, S. N. (2000). Plant litter and soil reflectance. *Remote Sensing of Environment*, 71(2):207–215.

Nagler, P. L., Inoue, Y., Glenn, E. P., Russ, A. L., and Daughtry, C. S. T. (2003). Cellulose absorption index (cai) to quantify mixed soil-plant litter scenes. *Remote Sensing of Environment*, 87(2-3):310–325.

Novozamsky, I., Houba, V., van Eck, R., and van Vark, W. (1983). A. novel digestion technique for multi-element plant analysis. *Communications in Soil Science and Plant Analysis*, 14:239–249.

Okin, G. S., Roberts, D. A., Murray, B., and Okin, W. J. (2001). Practical limits on hyperspectral vegetation discrimination in arid and semiarid environments. *Remote Sensing of Environment*, 77(2):212–225.

Ollinger, S. V. and Smith, M. L. (2005). Net primary production and canopy nitrogen in a temperate forest landscape: An analysis using imaging spectroscopy, modeling and field data. *Ecosystems*, 8(7):760–778.

Ollinger, S. V., Smith, M. L., Martin, M. E., Hallett, R. A., Goodale, C. L., and Aber, J. D. (2002). Regional variation in foliar chemistry and n cycling among forests of diverse history and composition. *Ecology*, 83(2):339–355.

Osborne, S. L., Schepers, J. S., Francis, D. D., and Schlemmer, M. R. (2002). Detection of phosphorus and nitrogen deficiencies in corn using spectral radiance measurements. *Agron J*, 94(6):1215–1221.

Owen-Smith, N. (2008). *Resource Ecology: Spatial and temporal dynamics of foraging*, Chapter: Effects of temporal variability in resources on foraging behaviour, pages 159–181. Springer.

Owen-Smith, N. and Danckwerts, J. (1997). *Vegetation of southern Africa*, Chapter: Herbivory, pages 397–420. Cambridge University Press, Cambridge.

Peckham, S. D., Ahl, D. E., Serbin, S. P., and Gower, S. T. (2008). Fire-induced changes in green-up and leaf maturity of the canadian boreal forest. *Remote Sensing of Environment*, 112(9):3594–3603.

Peterson, D. L., Aber, J. D., Matson, P. A., Card, D. H., Swanberg, N., Wessman, C., and Spanner, M. (1988). Remote sensing of forest canopy and leaf biochemical contents. *Remote Sensing of Environment*, 24(1):85–108.

Peterson, D. l. and Hubbard, G. S. (1992). Scientific issues and potential remote-sensing requirements for plant biochemical content. *Journal of Imaging Science and Technology*, 36:446–456.

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J.-M., Tucker, C. J., and Stenseth, N. C. (2005). Using the satellite-derived ndvi to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, 20(9):503–510.

Pretorius, Y. (2009). *Satisfying giant appetites : mechanisms of small scale foraging by large African herbivores*. PhD thesis, Resource Ecology Group.

Prins, H. H. T. (1996). *Ecology and Behaviour of the African Buffalo: Social inequality and decision making*. Wildlife Ecology and Behavioural Series. Chapman and Hall, London.

Prins, H. H. T. and Beekman, J. (1989). A balanced diet as a goal for grazing: the food of the manyara buffalo. *African Journal of Ecology*, 27:241–259.

Prins, H. H. T. and van Langevelde, F. (2008a). *Resource Ecology: Spatial and temporal dynamics of foraging*, Chapter: Assembling a diet from different places, pages 129–158. Springer.

Prins, H. H. T. and van Langevelde, F. (2008b). *Resource Ecology: Spatial and temporal dynamics of foraging*. Springer.

Provenza, F. D. (1995). Postingestive feedback as an elementary determinant of food preference and intake in ruminants. *Journal of Range Management*, 48(1):2–17.

Provenza, F. D., Villalba, J. J., Dziba, L. E., Atwood, S. B., and Banner, R. E. (2003). Linking herbivore experience, varied diets, and plant biochemical diversity. *Small Ruminant Research*, 49(3):257–274.

Qi, J., Chehbouni, A., Huete, A., Kerr, Y., and Sorooshian, S. (1994). A modified soil adjusted vegetation index. *Remote Sensing of Environment*, 48(2):119–126.

R Development Core Team, (2008). *R: A Language and Environment for Statistical*

Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Reed, B. C., Brown, J. F., VanderZee, D., Loveland, T. R., Merchant, J. W., and Ohlen, D. O. (1994). Measuring phenological variability from satellite imagery. *Journal of Vegetation Science*, 5(5):703–714.

Ribeiro da Luz, B. and Crowley, J. K. (2010). Identification of plant species by using high spatial and spectral resolution thermal infrared (8.0-13.5[mu]m) imagery. *Remote Sensing of Environment*, 114(2):404–413.

Rumelhart, D., Hinton, G., and Williams, R. (1986). *Parallel Distributed Processing: Explorations in the Microstructures of Cognition*, volume 1, Chapter: Learning internal representations by error propagation, pages 318–362. MIT Press, Cambridge, MA.

Salisbury, F. and Ross, C. (1992). *Plant Physiology*. Wadsworth Publishing Company, Belmont, 4th edition.

Schachtman, D. P., Reid, R. J., and Ayling, S. M. (1998). Phosphorus uptake by plants: From soil to cell. *Plant Physiology*, 116(2):447–453.

Schaepman, M. E., Koetz, B., Schaepman-Strub, G., and Itten, K. I. (2005). Spectrodirectional remote sensing for the improved estimation of biophysical and -chemical variables: two case studies. *International Journal of Applied Earth Observation and Geoinformation*, 6(3-4):271–282.

Schmidt, K. S. and Skidmore, A. K. (2001). Exploring spectral discrimination of grass species in african rangelands. *International Journal of Remote Sensing*, 22(17):3421–3434.

Schmidt, K. S. and Skidmore, A. K. (2003). Spectral discrimination of vegetation types in a coastal wetland. *Remote Sensing of Environment*, 85(1):92–108.

Schut, A. G. T., Lokhorst, C., Hendriks, M. M. W. B., Kornet, J. G., and Kasper, G. (2005). Potential of imaging spectroscopy as tool for pasture management. *Grass & Forage Science*, 60(1):34–45.

Scott, D. (1992). *Multivariate density estimation: Theory, practice and visualization*, Chapter: The curse of dimensionality and dimension reduction, pages 195–217. Wiley series in probability and mathematical statistics: Applied probability and statistics section. Wiley Inter-science.

Seagle, S. W. and McNaughton, S. J. (1992). Spatial variation in forage nutrient concentrations and the distribution of serengeti grazing ungulates. *Landscape Ecology*, 7(4):229–241.

Seastedt, T. R. (1988). Mass, nitrogen, and phosphorus dynamics in foliage and root detritus of tallgrass prairie. *Ecology*, 69(1):59–65.

Serrano, L., Penuelas, J., and Ustin, S. L. (2002). Remote sensing of nitrogen and lignin in mediterranean vegetation from aviris data: Decomposing biochemical from structural signals. *Remote Sensing of Environment*, 81(2-3):355–364.

Skidmore, A. K., Ferwerda, J. G., Mutanga, O., Van Wieren, S. E., Peel, M., Grant, C. C., Prins, H. H. T, Balcik, F. B., and Venus, V. (2010). Forage

quality of savannas – simultaneously mapping foliar protein and polyphenols for trees and grass using hyperspectral imagery. *Remote Sensing of Environment*, 114(1):64–72.

Skidmore, A. K., Turner, B. J., Brinkhof, W., and Knowles, E. (1997). Performance of a neural network: Mapping forests using gis and remotely sensed data. *Photogrammetric Engineering And Remote Sensing*, 63(5):501–514.

Smith, M. L., Ollinger, S. V., Martin, M. E., Aber, J. D., Hallett, R. A., and Goodale, C. L. (2002). Direct estimation of aboveground forest productivity through hyperspectral remote sensing of canopy nitrogen. *Ecological Applications*, 12(5):1286–1302.

Soukupova, J., Rock, B. N., and Albrechtova, J. (2002). Spectral characteristics of lignin and soluble phenolics in the near infrared- a comparative study. *International Journal of Remote Sensing*, 23(15):3039–3055.

Starks, P. J., Coleman, S. W., and Phillips, W. A. (2004). Determination of forage chemical composition using remote sensing. *Journal of Range Management*, 57(6):635–640.

Suzuki, Y., Tanaka, K., Kato, W., Okamoto, H., Kataoka, T., Shimada, H., Sugiura, T., and Shima, E. (2008). Field mapping of chemical composition of forage using hyperspectral imaging in a grass meadow. *Grassland Science*, 54(4):179–188.

Takahashi, W., Vu, N.-C., Kawaguchi, S., Minamiyama, M., and Ninomiya, S. (2000). Statistical models for prediction of dry weight and nitrogen accumulation based on visible and near-infrared hyper-spectral reflectance of rice canopies. *Plant Production Science*, 3:377–386.

Thenkabail, P. S., Smith, R. B., and De Pauw, E. (2000). Hyperspectral vegetation indices and their relationships with agricultural crop characteristics. *Remote Sensing of Environment*, 71(2):158–182.

Townsend, A. R., Cleveland, C. C., Asner, G. P., and Bustamante, M. M. C. (2007). Controls over foliar n:p ratios in tropical rain forests. *Ecology*, 88(1):107–118.

Treydte, A. C., Heitkönig, I. M., and Ludwig, F. (2009). Modelling ungulate dependence on higher quality forage under large trees in african savannahs. *Basic and Applied Ecology*, 10(2):161–169.

Treydte, A. C., Heitkönig, I. M., Prins, H. H. T., and Ludwig, F. (2007). Trees improve grass quality for herbivores in african savannas. *Perspectives in Plant Ecology, Evolution and Systematics*, 8(4):197 – 205.

Treydte, A. C., van Beeck, F. L., Ludwig, F., and Heitkönig, I. M. (2008). Improved quality of beneath-canopy grass in south african savannas: Local and seasonal variation. *Journal of Vegetation Science*, 19(5):663–670.

Tucker, C. J. (1979). Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*, 8(2):127–150.

Uno, Y., Prasher, S. O., Lacroix, R., Goel, P. K., Karimi, Y., Viau, A., and Patel,

R. M. (2005). Artificial neural networks to predict corn yield from compact airborne spectrographic imager data. *Computers And Electronics In Agriculture*, 47(2):149–161.

Ustin, S. L. (2004). *Remote sensing for natural resource management and environmental monitoring*, volume 4 of *Manual of remote sensing*. Wiley & Sons, Hoboken etc., third edition edition.

Ustin, S. L., Gitelson, A., Jacquemoud, S., Schaepman, M., Asner, G. P., Gamon, J. A., and Zarco-Tejada, P. (2009). Retrieval of foliar information about plant pigment systems from high resolution spectroscopy. *Remote Sensing of Environment*, 113(Supplement 1):S67–S77.

Vaiphasa, C., Skidmore, A. K., de Boer, W. F., and Vaiphasa, T. (2007). A hyperspectral band selector for plant species discrimination. *ISPRS Journal of Photogrammetry and Remote Sensing*, 62(3):225–235.

van de Vijver, C., Poot, P., and Prins, H. H. T. (1999). Causes of increased nutrient concentrations in post-fire regrowth in an east african savanna. *Plant and Soil*, 214(1):173–185.

van der Meer, F., de Jong, S., and Bakker, W. (2001). *Imaging Spectrometry*, Chapter: Imaging spectrometry: Basic analytical techniques, pages 17–61. Kluwer Academic Publishers.

van Oudtshoorn, F. (1992). *Guide to grasses of South Africa*. Briza Publisher, Arcadia.

van Soest, P. J. (1996). Allometry and ecology of feeding behavior and digestive capacity in herbivores: A review. *Zoo Biology*, 15(5):455–479.

Venter, F. (1990). *A classification of land for management planning in the Kruger National Park*. Phd Thesis, University of South Africa.

Wehrens, R. and Mevik, B.-H. (2007). *pls: Partial Least Squares Regression (PLSR) and Principal Component Regression (PCR)*. R package version 2.1-0.

Werner, P., editor (1991). *Savanna ecology and Management: Australian perspectives and intercontinental comparisons*. Blackwell Scientific Publishing.

Wessman, C., Aber, J., Peterson, D., and Melillo, J. (1988). Remote sensing of canopy chemistry and nitrogen cycling in temperate forest ecosystems. *Nature*, 335:154–156.

Yoder, B. J. and Pettigrew-Crosby, R. E. (1995). Predicting nitrogen and chlorophyll content and concentrations from reflectance spectra (400-2500 nm) at leaf and canopy scales. *Remote Sensing of Environment*, 53(3):199–211.

Zhang, X., Friedl, M. A., Schaaf, C. B., Strahler, A. H., Hodges, J. C. F., Gao, F., Reed, B. C., and Huete, A. (2003). Monitoring vegetation phenology using modis. *Remote Sensing of Environment*, 84(3):471–475.

Summary

The grazing resource provides the basis for maintenance of a broad spectrum of grazing herbivores, both wild and domestic. The quality of this resource, and thereby its ability to support herbivores, varies both spatially and temporally. Assessment of the forage resource has traditionally been made through point based studies. More recently with the development of imaging spectrometers it has become possible to create landscape level images depicting the concentrations of different plant nutrients. This study focussed on the grazing resource in an African savanna system located in the Kruger National Park, RSA. In this system, nitrogen and phosphorus are co-limiting nutrients, and the quantity of consumed fibre limits digestibility of forage. For rangeland managers knowledge on the concentrations of these nutrients is particularly relevant during the dry seasons when nutrients are limited.

The images created of plant nutrient concentrations have focussed on spatial variability in the wet season (i.e. plant growth periods). Spectral characteristics of plants vary between photosynthetic and non-photosynthetic tissues. It was the premise of this thesis that mapping of plant nutrients in the dry and wet seasons differed. In order to create a method that allowed for repeatable assessment of forage nutrients by imaging spectroscopy it was necessary to investigate the temporal aspect of nutrient variations. This thesis focussed on addressing temporal variations in forage nutrients and the implications for this on creating forage nutrient images of the grazing resource. Given the limitations of nitrogen and phosphorus, and the influence of fibre on the digestibility of forage, these three nutrients were selected as being representative of grazing forage quality.

To create nutrient models that can be repeatedly used it was necessary to understand the role and stability of variables in derived models. The theoretical framework for plant nutrient mapping with imaging spectroscopy (i.e. identification of absorption features) is founded in NIRS. In developing a model based on physical principals it was necessary to determine if at different measurement scales the physical variables (i.e. absorption features) were stable. Absorption features identified in NIRS studies have been used for developing and interpreting nutri-

ent models, however, the actual effects of upscaling these studies from laboratory to field level still required investigation. Using nitrogen as a base for analysis in chapter two, the effects of sample preparation and spectroscopic measurement on absorption feature stability were investigated. It was found that absorption features selected in models derived from dried and ground material were unsuitable to be used on vegetation canopies of fresh material (Chapter 2). In chapter five, it was however found that spectroscopic measurements taken of senescent grass canopies shared three nitrogen related absorption features (1020, 2060, and 2130 nm) with dried ground material models. It appears that for these absorption features, water and photosynthetic material, rather than leaf structure and canopy architecture affect their prominence for nitrogen prediction.

The combined findings of chapter 2 and chapter 5, support a wide body of literature that suggest that at the vegetation canopy level, subtle nutrient absorption features are masked by more prominent features (e.g. nitrogen features masked by water features). To understand temporal variations in nutrient modelling it was necessary to understand the effects of plant physiological changes on spectral modelling of nutrient variations. In ecological studies, phenological changes of vegetation have been shown to be linked to nutrient variations. Changes in a plants physiological state also result in spectral variations (e.g. reduction of water features as the water content in a plant declines). In chapter 3, using a greenhouse study it was established that plant age significantly influenced the selection of variables included in forage nutrient models. By either including plant age as an independent variable in modelling, or considering plant age when interpreting models lead to nutrient models that could be temporally applied.

Plant age, like nutrients vary across a landscape. Multiple factors cause these variations, e.g. topography, grazing, fires, etc. In chapter 3 it was established that knowledge of plant age aided the modelling of nutrients. Remote sensing has frequently been used for phenological studies and well established indices have been created to monitor phenological changes over time (e.g. NDVI, NDWI, CAI). It has, however, not been determined if these phenological indices were suitable for capturing plant age variations across a landscape. To suitably capture variations in plant age, the values derived from an index should chronologically follow the sequence of plant development. With such an index it would be possible to determine the landscape variation in plant age. In chapter 4, the potential of multiple phenological indices for capturing plant age variations were investigated. NDVI and NDWI could separate out age classes, but not chronologically, CAI and a newly proposed phenological index (PhIX) were both capable of chronologically separating out age classes. These two indices were therefore considered suitable for development of plant age images for use as input in nutrient models.

Using the greenhouse experiment it was possible to determine that plant age significantly contributed to explaining spectral variations in nutrient models (chapter 3).

In the field, temporal and spatial variations of nutrients will be the result of many additional factors (chapter 1, figure 1.1). To make a model that can be consistently applied, the models should be kept as simple as possible while retaining variables that make ecological and physical sense. In chapter 5, forage nutrient models, in a savanna system (Kruger National Park, RSA) were developed for both wet and dry seasons. Models were developed for each season using either ancillary (ecological) variables (that could be derived from RS products), or spectral absorption features related to the specific nutrient, or a combination of both. It was found that a suitable single model per nutrient could not be derived for multiple seasons, however, plant species and soil type, were variables that were significant, in most of the nutrient models. Besides these two base variables, differing additional variables were required to create each of the seasonal forage nutrient models.

Due to limitation of certain nutrients (e.g. nitrogen and phosphorus in the KNP), dry seasons are critical periods for grazing herbivores to obtain sufficient nutrients for maintenance. The studies discussed in chapters 2–5 provided evidence that it was possible to map forage nutrients using imaging spectroscopy in both the wet and dry seasons. Wavelengths selected in these studies have all included wavelengths located in the SWIR region. In chapter 6, it was investigated whether using a new imaging spectrometer (CAO Alpha system) that only covered the VNIR spectral range, it was possible to map forage nutrients in the dry season. It was found that during the dry season, by including ancillary variables and with the limited sensor spectral range (i.e. excluding the SWIR spectral region), it was possible to estimate the quantity of fibre and phosphorus with R^2 values above 60% and nitrogen with an R^2 value of 53%. Although, forage quality could be mapped using the VNIR region of the spectrum, to achieve higher accuracy models a full VNIR–SWIR spectrum is required.

In conclusion, this study verified that it was possible to map forage nutrients over a temporal range that includes both dry and wet seasons. Ideally a spectral range that extends from the visible through to the SWIR region should be used for nutrient mapping. By including ecological data (that can be created from spatial data) as ancillary variables in combination with physically linked (i.e. features linked to specific nutrients) absorption features, creates a framework for deriving ecologically sensible spatial and temporal models of forage nutrients.

Samenvatting

Graslanden zijn een natuurlijke hulpbron die de basis vormt voor het bestaan van een grote variëteit aan zowel wilde als gedomesticeerde herbivoren. De kwaliteit van het voedsel, en daarmee de mogelijkheid om herbivoren te ondersteunen, varieert zowel ruimtelijk als in tijd. Traditioneel werd voedselkwaliteit bepaald door middel van puntmetingen in het veld. Ontwikkeling van beeldvormende spectrometers maakt het nu mogelijk om op landschaps niveau ruimtelijke metingen van nutriëntenconcentraties in planten te maken. Het in dit proefschrift beschreven onderzoek richtte zich op een Afrikaans savannesysteem in het Kruger Nationaal Park, gelegen in de Republiek van Zuid Afrika. In dit gebied zijn stikstof en fosfor beide beperkt beschikbare nutriënten, terwijl de hoeveelheid geconsumeerde vezels de verteerbaarheid van voer beperkt. Het is van belang dat beheerders van weidegronden kennis hebben over deze nutriëntenconcentraties, met name in het droge seizoen, wanneer de hoeveelheid beschikbare nutriënten beperkt is.

De karteringen van nutriëntenconcentraties in planten die tot op heden gedaan zijn met aard observatie beschreven voornamelijk ruimtelijk variabiliteit in het natte seizoen. Dit is de groeiperiode voor vegetatie in het savanne ecosysteem. Spectrale kenmerken van planten variëren tussen fotosynthetische en niet-fotosynthetische weefsels. In dit proefschrift werd vooropgesteld dat het karteren van plant nutriënten in het natte of droge seizoen verschilt. Om een methode te ontwikkelen waarbij beeldvormende spectrometers zonder tijdsbeperking gebruikt kunnen worden om nutriënten te karteren, was het nodig om eerst de variatie van nutriënten in de tijd te bestuderen. Dit proefschrift richtte zich daarom op het bestuderen van variatie van voedingsstoffen in de tijd en de resulterende gevolgen voor het karteren van deze nutriënten. De beperkt beschikbare nutriënten stikstof en fosfor, en de invloed van vezels op de verteerbaarheid van voer, zijn een goede graadmeter van de voedingskwaliteit van grassen.

Om nutriëntenmodellen te maken die voor monitoring gebruikt kunnen worden, is het nodig om de rol en stabiliteit van variabelen in deze modellen te begrijpen. Het theoretische kader voor het karteren van plantnutriënten met behulp van beeldvormende spectroscopie (het identificeren van kenmerkende spectrale absorptie) is

gebaseerd op spectroscopie in het nabij-infrarode golflengtebereik (NIRS). Bij het ontwikkelen van een model dat gebaseerd is op fysische principes, mogen fysische variabelen (de kenmerkende absorptie golflengtes) niet veranderen bij waarneming op verschillende schaalniveaus. Absorptie golflengtes die gevonden zijn door onderzoek met NIRS zijn weliswaar gebruikt voor ontwikkeling en interpretatie van nutriëntmodellen, maar het effect van schaalvergroting van laboratorium waarnemingen naar veldwaarnemingen was nog niet voldoende onderzocht. Door gebruik te maken van stikstof als basis voor de analyse, zoals beschreven in hoofdstuk 2, kon de invloed van monster preparatie van plant materiaal en de spectrale meetopstelling onderzocht worden. Uit de resultaten bleek dat het niet mogelijk was om de spectrale absorptie kenmerken van gedroogd en gemalen plant materiaal te relateren aan een natuurlijke bedekking met levend plant materiaal (hoofdstuk 2). In hoofdstuk 5 bleek echter wel dat spectrale absorptiekenmerken (bij 1020, 2060, en 2130 nm golflengte), van een ouder grasland konden worden gerelateerde aan modellen die gebaseerd waren op gedroogd en gemalen plant materiaal. Het bleek dat voor deze drie absorptie golflengtes, water en fotosynthetisch materiaal van grotere invloed waren bij het voorspellen van stikstof gehalte dan bladstruktuur en bedekkingsstruktuur.

De resultaten van hoofdstukken 2 en 5 passen in het beeld dat geschetst wordt in de literatuur, namelijk dat op het schaalniveau van vegetatie, de subtiele spectrale absorptie kenmerken van nutriënten overschaduwd worden door andere, prominentere, kenmerken (bijvoorbeeld absorptie door stikstof gemaskeerd door absorptie door water). Om de variatie van nutriëntenconcentraties in de tijd te begrijpen, was het nodig om eerst de effecten van fysiologische veranderingen van planten op spectrale nutriëntenmodellen te beschrijven. Ecologisch onderzoek heeft laten zien dat fenologische veranderingen in vegetatie gerelateerd zijn aan veranderingen in nutriëntconcentraties in plantweefsel. Veranderingen in de fysiologische staat en nutriëntenconcentraties van een plant resulteert vervolgens weer in spectrale veranderingen (bijv. een vermindering van water absorptie bij een afnemende hoeveelheid water in een plant). In hoofdstuk 3 werd door middel van een kas experiment vastgesteld dat de plant leeftijd een significante invloed heeft op de keuze van variabelen in nutriëntmodellen, voor stikstof, fosfor en vesels. Door de leeftijd van een plant als onafhankelijke variabele op te nemen bij het maken van een model, of door plant leeftijd te gebruiken bij het interpreteren van een modelresultaat, kan een nutriëntmodel voor metingen over langere tijd gebruikt worden.

Op landschapsniveau komen planten van verschillende leeftijden voor. Dit beinvloed de concentraties van nutriënten. Verscheidene factoren beinvloeden de plant leeftijd, zoals, topografie, begrazing, brand, enz.. In hoofdstuk 3 werd vastgesteld dat kennis omtrent de leeftijd van planten helpt bij het modelleren van nutriënten. Aardobservatie werd al eerder gebruikt voor fenologisch onderzoek en verscheidene indices zijn gedefinieerd voor het observeren van fenologische veranderingen

in planten over tijd (bijv. NDVI, NDWI, CAI). Het was echter nog niet vastgesteld of deze indices geschikt zijn voor het bepalen van ruimtelijke variatie in plantleeftijd op landschapsniveau. Om de variatie in plantleeftijd deugdelijk vast te stellen, moet een vegetatie index de chronologische ontwikkeling van een plant kunnen volgen. In hoofdstuk 4 werd gekeken naar de geschiktheid van verscheidene fenologische indices voor het bepalen van plant leeftijd. NDVI en NDWI konden onderscheid maken in leeftijdscategorieën, maar niet in een chronologische volgorde. CAI en een nieuw ontwikkelde index, PhIX, konden beide wel leeftijdscategorieën onderscheiden in een chronologische volgorde. Deze laatste twee indices waren dus geschikt voor het karteren van plantleeftijd met optisch beeldmateriaal en gebruik in nutriëntmodellen.

Door het kas experiment was het mogelijk om vast te stellen dat leeftijd van planten significant bijdraagt aan het verklaren van de spectrale variatie in de nutriëntmodellen (hoofdstuk 3). In het veld echter wordt variatie in nutriënten en spectrale waarden ook door verscheidene andere factoren bepaalt (hoofdstuk 1, figuur 1.1). Om een model robuust te maken, moet het eenvoudig zijn maar moet alle relevante variabelen met ecologische en fysische informatie bevatten. In hoofdstuk 5 werden nutriëntenmodellen ontwikkeld voor zowel het natte als het droge seizoen in het savanne syteem van het Kruger Nationaal Park. Deze modellen werden apart gemaakt voor elk seizoen, gebruik makend van ofwel ecologische variabelen (verkregen door aardobservatie), ofwel spectrale absorptiekenmerken die gerelateerd zijn aan een bepaalde nutriënt, ofwel een combinatie van beide. Het was niet mogelijk om een enkel model te maken dat geschikt is voor iedere nutriënt en geschikt is voor zowel het droge als het natte seizoen. Het bleek ook dat plantensoort en bodemtype in het droge en het natte seizoen significante variabelen zijn in de meeste modellen. Naast deze twee variabelen waren nog andere variabelen nodig om een seizoensonafhankelijk nutriëntenmodel te maken.

Door de beperkte beschikbaarheid van bepaalde nutriënten (zoals bijv. stikstof en fosfor in het Kruger Nationaal Park), zijn de droge seizoenen kritieke periodes voor grazende herbivoren om voldoende voedingsstoffen binnen te krijgen. Het onderzoek, beschreven in hoofdstukken 2 tot en met 5, liet zien dat het zowel in het natte als het droge seizoen mogelijk is om voedingsstoffen te karteren met behulp van beeldvormende spectroscopie. In dit onderzoek zijn significante golflengtes gevonden in het kortgolvig infrarode (SWIR) golflengte bereik die gebruikt kunnen worder voor het karteren van nutriënten. In hoofdstuk 6 werd onderzocht of de nieuwe, vliegtuig gedragen, CAO Alpha beeldvormende spectrometer, met enkel banden in het zichtbare en nabij infrarode (VNIR) golflengte bereik, voedingsstoffen kon karteren in het droge seizoen. Ondanks dat het SWIR golflengte bereik niet aanwezig was in deze sensor, bleek dat, door gebruik te maken van ecologische variabelen, het mogelijk was om de hoeveelheid vezels en fosfor met R^2 waardes boven de 60% te karteren, en stikstof met R^2 waardes van 53%. Hoewel de kwaliteit van voedingsstoffen gekarteerd kon worden met enkel het VNIR golflengte

bereik, zal een volledig VNIR–SWIR golflengte bereik nodig zijn om een hogere nauwkeurigheid te verkrijgen.

Samenvattend, dit onderzoek heeft laten zien dat het mogelijk is om voedingsstoffen te karteren over een tijdsperiode die zowel het natte als het droge seizoen omvat. Idealiter zou zowel het zichtbare, nabij-infrarode en kortgolvig infrarode golflengte bereik gebruikt moeten worden voor het karteren van nutriënten. Het is de combinatie van ecologische variabelen en physiche variabelen de het mogelijk maakt om natuurlijke voedingsstoffen in savanne graslanden in ruimte en tijd to karteren.

Publications

1. **Knox, N.M.**, Skidmore, A. K., Schlerf, M., de Boer, W.F., van Wieren, S.E., van der Waal, C., Prins, H.H.T. and Slotow, R. (2010). Nitrogen prediction in grasses: Effect of bandwidth and plant material state on absorption feature selection. *International Journal of Remote Sensing*, 31(3): 691 704.

2. **Knox, N. M.**, Skidmore, A. K., Schlerf, M., Groen, T. A., Prins, H. H. T., van Wieren, S. E., van Langevelde, F., de Boer, W. F., Heitkönig, I. M., Mwakiwa, E., Pretorius, Y., Grant, C., and Slotow, R.. The influence of plant age, on predicting forage-nutrient concentrations derived from spectroradiometric data. Resubmitted, after revision to: *International Journal of Applied Earth Observation and Geo-information.*

3. **Knox, N.M.**, Skidmore, A. K., van der Werff, H.M.A., Groen, T.A., de Boer, W.F., Prins, H.H.T., Kohi, E.M., Peel, M.. A comparison of spectroscopic phenological algorithms for the differentiation of plant age in savanna grasses. Resubmitted, after revision to: *International Journal of Remote Sensing.*

4. **Knox, N.M.**, Skidmore, A.K., Asner, G.P., Prins, H.H.T., van der Werff, H.M.A., de Boer, W.F., van der Waal, C., de Knegt, H.J., Kohi, E.M., Slotow, R.. Mapping savanna forage quality, in the dry season, using CAO Alpha imagery. In review: *Remote Sensing of Environment.*

5. Kohi, E.M., de Boer, W.F., Slot, M., van Wieren, S.E., Ferwerda, J.G., Grant, C., Heitkönig, I.M., de Knegt, H.J., **Knox, N.M.**, van Langevelde, F., Peel, M., Slotow, R., van der Waal, C., Prins, H.H.T.

(2010). Effects of simulated browsing on growth and leaf chemical properties in Colophospermum mopane saplings. *African Journal of Ecology*, 48(1): 190-196.

6. de Knegt, H.J., van Langevelde, F., Coughenour, M.B., Skidmore, A. K., de Boer, W.F., Heitkönig, I.M., **Knox, N.M.**, Kohi, E.M., Peel, M., Slotow, R., van der Waal, C., van Wieren, S.E., Prins, H.H.T. Spatial autocorrelation and the scaling of species-environment relationships. In press: *Ecology*.

7. de Knegt, H.J., van Langevelde, F., Skidmore, A. K., Delsink, A., Slotow, R., Henley, S., Bucini, G., de Boer, W.F., Coughenour, M.B., Grant, C.C., Heitkönig, I.M.A., Henley, M., **Knox, N.M.**, Kohi, E.M., Mwakiwa, E., Page, B.R., Peel, M., Pretorius, Y., van Wieren, S.E., Prins, H.H.T. The spatial scaling of habitat selection by African elephants. In press: *Journal of Animal Ecology*.

Biography

Nichola (Nicky) Maria Knox was born in Johannesburg, South Africa on 30 November 1973. In 1991, she completed her secondary education at De La Salle Holy Cross College, Victory Park. Having always had a keen interest in biology, animals and wildlife, she chose to extend this interest and study in this direction. She went to the University of Natal, Pietermaritzburg where at the end of 1994 she obtained her Bachelor of Science degree, majoring in Zoology and Botany. After working and traveling in Europe and the USA, in 1998 she returned back to South Africa to study for a BSc (Hons) in Wildlife Management, at the University of Pretoria. Following the completion of this degree she worked (teaching and research) and travelled in the USA and Honduras. In early 2000 she moved to Windhoek, Namibia to work for the Land Management Department at the Polytechnic of Namibia. Here her work focused on teaching Rural Land Use Planning. She took sabbatical leave in 2002-2003 to study at the International Institute for Geo-information Science and Earth Observation (ITC), The Netherlands, graduating with an MSc *Cum Laude* in Earth Observation for Earth Systems Analysis and Management. This study culminated in an MSc thesis entitled "An assessment of techniques used for mapping lichen fields, RSA". She returned to Namibia to continue working as a lecturer. On her return to Namibia, under the guidance of Prof A.K. Skidmore, they applied for an NWO-WOTRO PhD fellowship. The fellowship was awarded and resulted in her returning to ITC, in mid 2005, to embark on a PhD study. This thesis is the result of this study.

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (4.5 ECTS)
- Vegetation resource distribution and dynamics assessed using hyperspectral remote sensing, and its impact on wildlife (2005/2006)

Writing of project proposal (4 ECTS)
- Research proposal: vegetation resource distribution and dynamics assessed using hyperspectral remote sensing, and its impact on wildlife (2005)

Post-graduate courses (3 ECTS)
- IDL Programming course; ITC (2007)
- Advanced statistics; WUR (2008)

Laboratory training and working visits (1.8 ECTS)
- Leaf biochemical analysis; WUR (2006)
- Greenhouse skills; WUR (2006)

Competence strengthening / skills courses (3 ECTS)
- Scientific skills-presentations (2006)
- Scientific skills-writing (2006)

PE&RC Annual meetings, seminars and the PE&RC weekend (3 ECTS)
- PE&RC Weekend (2006)
- ITC Seminars-various topics (2009)
- ITC PhD Weekend (also assisted with organisation) (2009)

Discussion groups/ local seminars/ other scientific meetings (6.9 ECTS)
- REG Discussion seminars (2005)
- NRS PhD Bi-weekly discussion/tutorial group (assisted with organisation of tutorial for in 2007) (2005-2010)
- Tropical Ecology PhD day seminar; University Amsterdam (2008)

International symposia, workshops and conferences (11.5 ECTS)
- KNP Network meeting, presentations (2005, 2006, 2008)
- IGARSS, poster; Boston (2008)
- IGARSS, presentation; South Africa (2009)

ITC Dissertation List

http://www2.itc.nl/research/phd/phd_graduates.aspx