FORAGE SUPPLY OF WEST AFRICAN RANGELANDS:
TOWARDS A BETTER UNDERSTANDING OF ECOSYSTEM SERVICES BY APPLICATION OF HYPERSPECTRAL REMOTE SENSING

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Jessica Ferner
aus
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Zusammensetzung der Promotionskommission

1. Gutachter: Prof. Dr. Sebastian Schmidtlein

2. Gutachter: Prof. Dr. Klaus Greve

Fachnahes Mitglied: PD Dr. Anja Linstädter

Fachfremdes Mitglied: Prof. Dr. Gerhard von der Emde

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ABBREVIATIONS

ADF	Acid detergent fibre
AM	Amplitude modulation
aNDF	Amylase-treated neutral detergent fibre
AIC	Akaike information criterion
BM	(Green) biomass
BMBF	German Federal Ministry of Education and Research
C	Carbon
CCA	Canonical correspondence/correlation analysis
CO_2	Carbon dioxide
CP	Crude protein
DCAD	Dietary cation-anion difference
DM	Dry matter
EnMAP	Environmental mapping and analysis programme
EO-1	Earth-Observing 1 spacecraft
ES	Ecosystem service
ESA	European Space Agency
FieldSpec	ASD (now Malvern Panalytical) FieldSpec® 3 fieldspectroradiometer
FM	Frequency modulation
FWHM	Full-width-half-maximum
gBM	Green biomass
GP	Gas production
HANPP	Human appropriation of net primary productivity
HGT	Hohenheim gas test
HypXIM	Hyperspectral X IMagery
HyspIRI	Hyperspectral Infrared Imager
IPCC	Intergovernmental panel on climate change
IR	Infrared
K	Potassium
LAI	Leaf area index
LiDAR	Light detection and ranging
LV	Latent variable
LWIR	Longwave infrared (region of the electromagnetic spectrum)

MAP	Mean annual precipitation
ME	Metabolisable energy
MESMA	Multiple endmember spectral mixture analysis
MEY	Metabolisable energy yield
MODIS	Moderate resolution imaging spectroradiometer
MSI	Multi-spectral instrument
MWIR	Midwave infrared (region of the electromagnetic spectrum)
N	Nitrogen
NDF	Neutral detergent fibre
NDVI	Normalized difference vegetation index
NIR	Near infrared (region of the electromagnetic spectrum)
NPAV	Non-photosynthetic active vegetation
OMD	Organic matter digestibility
P	Phosphorus
PAV	Photosynthetic active vegetation
PCA	Principal component analysis
PLSR	Partial least-squares regression
PLS-PM	Partial least squares path modelling
RS	Remote sensing
SAR	Synthetic aperture radar
SEM	Structural equation modelling
SES	Social-ecological system
SHALOM	Spaceborne hyperspectral applicative land and ocean mission
SRES	Special report on emissions scenarios
SWIR	Shortwave infrared (region of the electromagnetic spectrum)
tBM	Total aboveground biomass
THz	Terahertz radiation
USGS	United States Geological Survey
UV	Ultraviolet (region of the electromagnetic spectrum)
VAL	Validation
VIS	Visible (region of the electromagnetic spectrum)
VLWIR	Very longwave infrared (region of the electromagnetic spectrum)
VNIR	Visible and near-infrared (region of the electromagnetic spectrum)
XA	Ash

SUMMARY

Grazing is the predominant type of land use in savanna regions all over the world. Although large savanna areas in Africa are still grazed by wild herbivores, the West African Sudanian savanna region mainly comprises rangeland ecosystems, providing the important ecosystem service of forage supply for domestic livestock. However, these dryland rangelands are threatened by global change, including a predicted increase in climatic aridity and variability as well as land degradation caused by overgrazing. In this context, the international research project WASCAL (West African Science Service Centre on Climate Change and Adapted Land Use) was initiated to investigate the effects of climatic change in this region and to develop effective adaptation and mitigation measures.

This cumulative dissertation aims at providing a methodology for a regular knowledge-driven monitoring of forage resources in West Africa. Due to the vast and remote nature of Sudanian savannas, remote sensing technologies are required to achieve this goal. Hence, as a first step, it was necessary to test whether hyperspectral near-surface remote sensing offers the means to model and estimate the two most important aspects of forage supply, i.e. forage quantity (green biomass) and quality (metabolisable energy) (**Chapter 2.1**). Evidence was provided that partial least squares regression was able to generate robust and transferable forage models. In a second step, direct and indirect drivers of forage supply on the plot and site level were identified by using path modelling within the well-defined concept of social-ecological systems (**Chapter 2.2**). Results indicate that the provisioning ecosystem service of forage supply is mainly driven by land use, while climatic aridity exerts foremost indirect control by determining the way people use their environment. Building on these findings, upscaling of models was tested to generate maps of forage quality and quantity from satellite images (**Chapter 2.3**). Here, two different available data sources, i.e. multi- and hyperspectral satellites, were compared to serve the overall objective to install a regular forage monitoring system. In conclusion, preliminary forage maps could be created from both systems. An independent validation would be a research desiderate for future studies. Moreover, both systems feature certain shortcomings that might only be overcome by future satellite missions.

ZUSAMMENFASSUNG

Die Beweidung stellt die dominierende Landnutzungsart in den Savannengebieten der Erde dar. Auch wenn weite Savannengebiete Afrikas heute noch von wildlebenden Herbivoren beweidet werden, so besteht die Westafrikanische Sudan Savanne hauptsächlich aus anthropogen genutzten Weideökosystemen, welche die bedeutende Ökosystemdienstleistung der Futterbereitstellung für domestizierte Nutztiere liefern. Die Weideländer der Trockengebiete sind allerdings durch den globalen Wandel in Gefahr, insbesondere durch einen prognostizierten Anstieg klimatischer Aridität und Variabilität sowie durch Landdegradation durch Überweidung. In diesem Kontext wurde das internationale Forschungsprojekt WASCAL (West African Science Service Centre on Climate Change and Adapted Land Use) initiiert, um die Auswirkungen des Klimawandels in dieser Region zu untersuchen und effektive Anpassungs- und Abschwächungsmaßnahmen zu entwickeln.

Diese kumulative Dissertation hat das Ziel, eine Methode für ein regelmäßiges wissensbasiertes Monitoring der Futterressourcen Westafrikas zu erarbeiten. Durch die Weite und Abgeschiedenheit der Sudan Savanne werden zu diesem Zweck Fernerkundungstechnologien benötigt. Von daher wurde in einem ersten Schritt getestet, ob die hyperspektrale oberflächennahe Fernerkundung Möglichkeiten bietet, um die zwei wichtigsten Aspekte der Futterbereitstellung, d.h. Futterquantität (grüne Biomasse) und -qualität (metabolisierbare Energie) zu modellieren (**Kapitel 2.1**). Es konnte gezeigt werden, dass die Regressionsmethode der kleinsten Quadrate (Partial Least Squares Regression) in der Lage war, robuste und übertragbare Futtermodelle zu generieren. In einem zweiten Schritt wurden direkte und indirekte Treiber der Futterbereitstellung auf dem Level von Untersuchungsfläche und -standort mit Hilfe von Pfadmodellierung innerhalb des klar definierten Konzepts der sozial-ökologischen Systeme identifiziert (**Kapitel 2.2**). Die Ergebnisse weisen darauf hin, dass die zu den bereitstellenden Ökosystemdienstleistungen gehörende Dienstleistung der Futterbereitstellung hauptsächlich von der Landnutzung beeinflusst wird. Klimatische Aridität übt hingegen eine weitestgehend indirekte Kontrolle aus, indem sie beeinflusst, wie Menschen ihre Umwelt nutzen.

Aufbauend auf diesen Ergebnissen wurde anschließend das Hochskalieren der Futtermodelle getestet, um mit Hilfe von Satellitenbildern Karten von Futterqualität und -quantität zu generieren (**Kapitel 2.3**). Dazu wurden multi- und hyperspektrale Satelliten als zwei unterschiedliche verfügbare Bildquellen verglichen und hinsichtlich ihrer Anwendbarkeit auf das übergeordnete Ziel der Installation eines regelmäßigen Monitorings für Futterressourcen untersucht. Zusammenfassend lässt sich sagen, dass basierend auf beiden Satellitensystemen erste Futterkarten erstellt werden konnten. Eine unabhängige Validierung der Ergebnisse in zukünftigen Studien wäre sinnvoll und wünschenswert. Des Weiteren weisen beide Satellitensysteme gewisse Defizite auf, welche erst durch zukünftige Satellitenmissionen überwunden werden dürften.

1 GENERAL INTRODUCTION

1.1 PREFACE

This doctoral study is embedded in the Core Research Programme of the WASCAL project (West African Science Service Centre on Climate Change and Adapted Land Use; *www.wascal.org*). The project is funded by the German Federal Ministry of Education and Research (BMBF) and aims to support research activities in ten West African countries and Germany that will enhance the resilience of human and environmental systems to climate change and increased climatic variability.

In West African savannas, grazing systems are among the most important components of land use systems, providing up to 44% of agricultural gross domestic product. It is estimated that 60 million heads of cattle and 160 small ruminants are living in West Africa and the Sahel zone, providing food and income for the poorest populations (SWAC-OECD/ECOWAS, 2008). The availability of forage resources is crucial for the livestock sector and thus plays a critical role in human nutrition and food security (Godber & Wall, 2014; Herrero & Thornton, 2013). A regular cost-effective and efficient monitoring of this vital natural resource would constitute a valuable service to the WASCAL project. Consequently, this doctoral study focuses on the provisioning ecosystem service of forage supply and aims at a deeper understanding of the scientific prerequisites needed to develop such a monitoring service by means of remote sensing technology that helps to tackle the challenges related to climate change in West Africa.

1.2 SAVANNAS AND RANGELANDS

The ecology of savanna ecosystems

Savannas form a tropical and subtropical biome (Hill & Hanan, 2010; Scholes & Walker, 2004) mostly defined by their vegetation composition as a mixture of grasses and trees in varying proportions (Sankaran et al., 2005). Climatically, savannas evolve in a wide range of conditions between 18.5 – 30°C mean annual temperature and 200 – 1700 mm mean annual precipitation (Lehmann et al., 2014). However, climatic attributes such as a marked alternation between dry and wet seasons lead to structural and functional characteristics that differentiate savannas from other biomes such as forests, grasslands, and deserts (Bourliere, 1983; Solbrig, Medina, & Silva, 1996). Although scientists agree on most of these predominant characteristics of savanna ecosystems, the exact definition and delimitation is still under discussion (Hill & Hanan, 2010; Scholes & Walker, 2004).

Combining savannas with tropical and subtropical grasslands and shrublands, Olson et al. (2001) delineated the global distribution of this biome (**Figure 1.2-1**) verging on the tropical rainforests at the equator (Shaw, Jacobs, & Everett, 2000). Depending on the exact definition, savannas cover one eighth (Oomen et al., 2016a) to one fifth (Scholes & Walker, 2004) of the world´s land surface and approximately 50% (Grace et al., 2006) to 65% (Walker & Noymeir, 1982) of Africa.

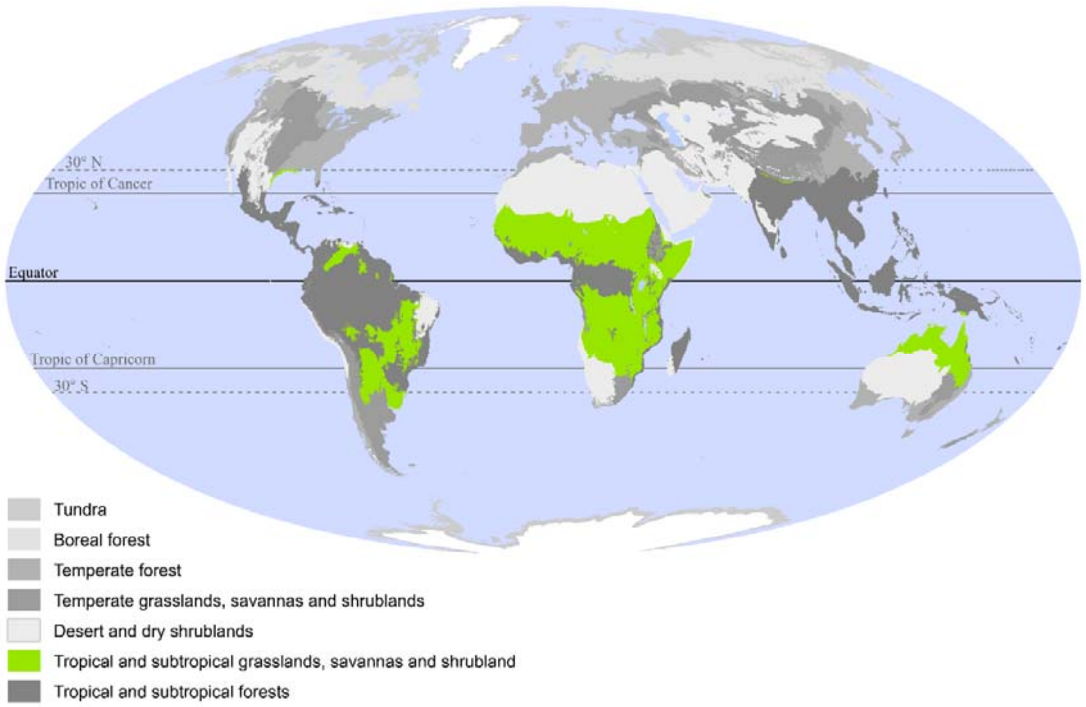

Figure 1.2-1: Global distribution of tropical and subtropical grasslands, savannas and shrublands as well as other main biomes based on data provided by Olson, Dinerstein et al. (2001). A common definition of the tropics is the region bounded by the Tropics of Cancer to the north and the Topics of Capricorn to the south. Savannas can be found between the equator and around 30° latitude (Scholes and Walker 2004).

Most savannas are structured as “savanna parklands”, i.e. landscapes with a mosaic of woody plant patches within a matrix of herbaceous vegetation (Menaut et al., 1990; San Jose, Farinas, & Rosales, 1991). Thus, the interaction of the woody layer and the mainly graminoid understory is an essential property of savanna ecosystems (Shaw et al., 2000). The herbaceous layer is dominated by fire tolerant and shade intolerant grasses featuring a C_4 photosynthetic pathway (**Box 1.2-1**; Ratnam et al. (2011)). This separates them from pure grasslands and forests, and savannas do not simply form a transitional vegetation type, neither in a geographical nor in an ecological sense (Scholes & Walker, 2004).

Competition for water is assumed to be a major factor in savanna ecosystems since all savannas are water limited at least for some part of the year (Scholes & Archer, 1997). Total precipitation amounts can vary widely but all savannas experience strong seasonal rainfall pattern with a hot rainy season and one (or two) pronounced dry season(s) during winter time (Solbrig, 1996; Walker & Noymeir, 1982).

The provision of ecosystem services, e.g. forage supply (Frank, McNaughton, & Tracy, 1998) as well as nutrient mineralisation, depends highly on water availability (Scholes & Walker, 2004). However, rainfall patterns are highly variable in time (intra- and inter-annually) and space (Frank et al., 1998; Hill & Hanan, 2010).

Box 1.2-1: C_4 Plants

Plants have developed different mechanisms of photosynthesis pathways. The majority of plants use the so called C_3 pathway. However, a group of plants, i.e. **C_4 plants**, of which sixty percent are grasses (Heckathorn, McNaughton, & Coleman, 1999), use a C_4 pathway where the plant is able to sustain a high concentration of carbon dioxide (CO_2) molecules around the C_3 photosynthetic machinery (Edwards et al., 2010). This is achieved by a relocation of specific steps of the photosynthesis mechanisms into different compartments of the leaf, which helps prevent photorespiration, i.e. the respiration of sugar phosphates back to carbon dioxide (www.britannica.com). As a consequence, C_4 plants are able to use sunlight more efficiently, particularly at high temperatures which makes them more competitive than C_3 plants in areas with high light, low water and low nutrient availability (Kellogg, 2013). However, C_4 grasses only outperform C_3 grasses at certain temperatures and concentrations of atmospheric CO_2 (**Figure 1.2-2**). Nonetheless, although C_4 plants comprise only 3% of vascular plant species, they account for ca. 25% of the terrestrial photosynthesis capacity (Edwards et al., 2010). Corn, sorghum, and sugarcane are examples of agronomically important C_4 crops.

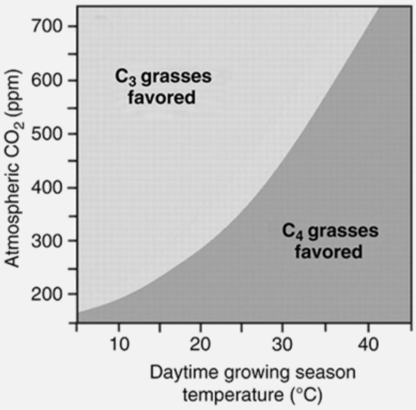

Figure 1.2-2: Influence of temperature and CO_2 concentration on the competitive behaviour of C_3 and C_4 grasses (figure from Ehleringer, Cerling, and Helliker (1997)). Under current CO_2 concentrations of around 400 ppm, C_4 grasses outperform C_3 grasses particularly in hot (sub)tropical environments like savanna ecosystems.

Savanna ecosystems develop on a variety of parent material where different intensities and durations of weathering processes may lead to diverse soil types (Hill & Hanan, 2010). This is most apparent in African savannas, spanning a wide range of abiotic site conditions resulting in considerable soil variation (Scholes & Walker, 2004). Some examples of common savanna soil types are Entisols, which are high in weatherable minerals, Alfisols, which tend to deplete in nutrients and Vertisols, fertile black cracking clays (Palm et al., 2007). Recurrent soil attributes under savannas are seasonal soil moisture stress, low nutrient storages, acidity, aluminium toxicity, high leaching potential as well as high soil erosion risk (Palm et al., 2007).

It is beyond controversy that savanna ecosystems are at least to some part caused, transformed and until today maintained by human activities. Some current vegetation patterns date from prehistoric anthropogenic land use (Scholes & Archer, 1997). However, intensification of land use such as clearing of trees for fuel, timber and agricultural activities led to a degradation of savannas (Sinclair & Fryxell, 1985; Young & Solbrig, 1993). Bush encroachment is a specific type of savanna degradation caused by fire suppression, reduction or extermination of indigenous animals often coupled with the introduction of livestock and exotic plants (Archer, 1994; Gardener, McIvor, & Williams, 1990). It is expected that climatic changes, agricultural expansions and changes in pastoral systems as well as fire management will cause a shift of savanna ecosystems, e.g. the transformation of tropical forests to open savanna landscapes (Barlow & Peres, 2008; Bond, 2008; Knapp et al., 2008) but also a conversion of former savanna grasslands to woodlands in absence of disturbances (Skowno et al., 2017).

Rangelands in savanna ecosystems

Around 25% of global land area is covered by rangelands (UNEP, 2016). Savannas comprise the majority of the world´s rangelands and livestock herds (Scholes & Archer, 1997) which is why these ecosystems are characterized by a very high biomass removal, e.g. almost 60% in the Serengeti (Frank et al., 1998). However, due to the low forage quality of the mainly C_4 grasses in savannas, animals face problems to meet their energy and nutritional requirements (McNaughton, 1990).

The expansion of agricultural cultivation in natural grasslands and savannas and the transformation into pastures and rangelands for domestic livestock (Frank et al., 1998) leads to a very high percentage of HANPP (human appropriation of net primary productivity), e.g. more than 20% in East and West African savannas (Hill & Hanan, 2010). Managed rangelands differ considerably from natural systems, especially in two aspects. Firstly, due to management efforts (e.g. predator protection and supplementary water, feed and nutrients) ungulate biomass often exceeds those of natural systems (Oesterheld, Sala, & McNaughton, 1992). Secondly, sedentary lifestyles and herding prevent seasonal migrations in response to spatio-temporal variability of forage supply, increasing the risk of overexploitation of resources and thus degradation processes (Frank et al., 1998). These differences might explain why natural grazing often has positive effects on ecosystem properties while domestic livestock grazing tends to have neutral or even negative effects (Milchunas & Lauenroth, 1993; Oesterheld et al., 1992).

Finally, savannas are not only the cradle of humankind and home to over a billion people (Mistry, 2000), but also ecosystems rich in (endemic) plant species (Kier et al., 2005; White, 1983). However, we still lack substantial knowledge of the abiotic and biotic factors shaping these ecosystems, limiting an in-depth investigation of the coupled human-environmental system (**Box 1.2-2**) of savanna biomes (Hill & Hanan, 2010).

Box 1.2-2: Coupled human–environmental systems

Coupled human–environmental systems (**Figure 1.2-3**) are also called social-ecological systems (SESs, www.resalliance.org). These systems are complex and characterised by mutual interactions between and among human activities (the social/human sub-system) and natural-world processes (the ecological/environmental sub-system) (Reynolds et al., 2007). Additionally, SESs are dynamic systems undergoing continuous changes which lead to a dynamic co-adaptation of human decision making and the environment's production of ecosystem services, i.e. the key linkages between sub-systems (Stafford Smith et al., 2007). A profound understanding of this co-adaptation or co-evolution and how it feeds back into the system´s capacity to adapt to global change is the prerequisite to developing and establishing a sustainable resource management (Rammel, Stagl, & Wilfing, 2007).

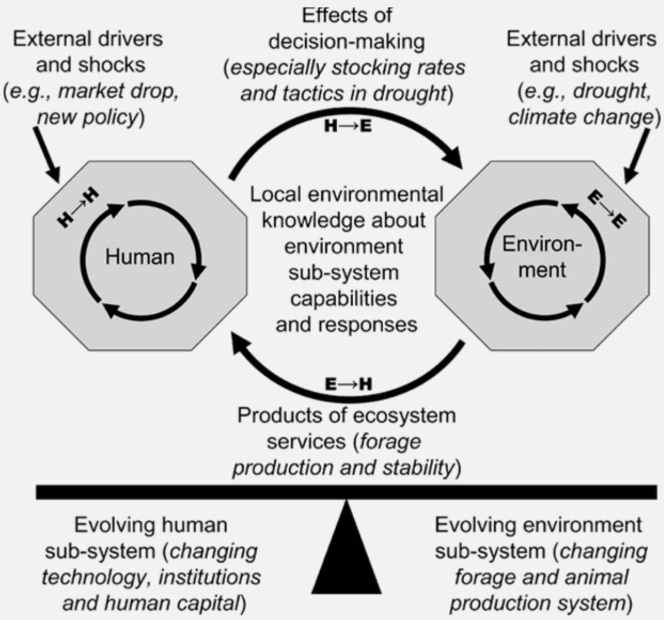

Figure 1.2-3: Conceptual framework by Stafford Smith et al. (2007) illustrating the coupled human-environmental system of dryland rangelands. The human (H→H) and the environmental sub-systems (E→E) are connected by key linkages, i.e. by effects of decision-making (H→E) and products of ecosystem services (E→H) moderated by local environmental knowledge. Linkages between, and modifications within, sub-systems have to evolve in a balanced way to allow for a dynamic co-adaptation.

The Sudanian Savanna of West Africa

This doctoral study focuses on Sudanian savanna ecosystems in West Africa. The region is characterized by a marked climatic gradient leading to vegetation zones from dense rain forest and semi-deciduous forest along the coastal belts to successive more open vegetation types to the north, i.e. Guinea savanna, Sudanian savanna and finally the Sahel zone (**Figure 1.2-4**).

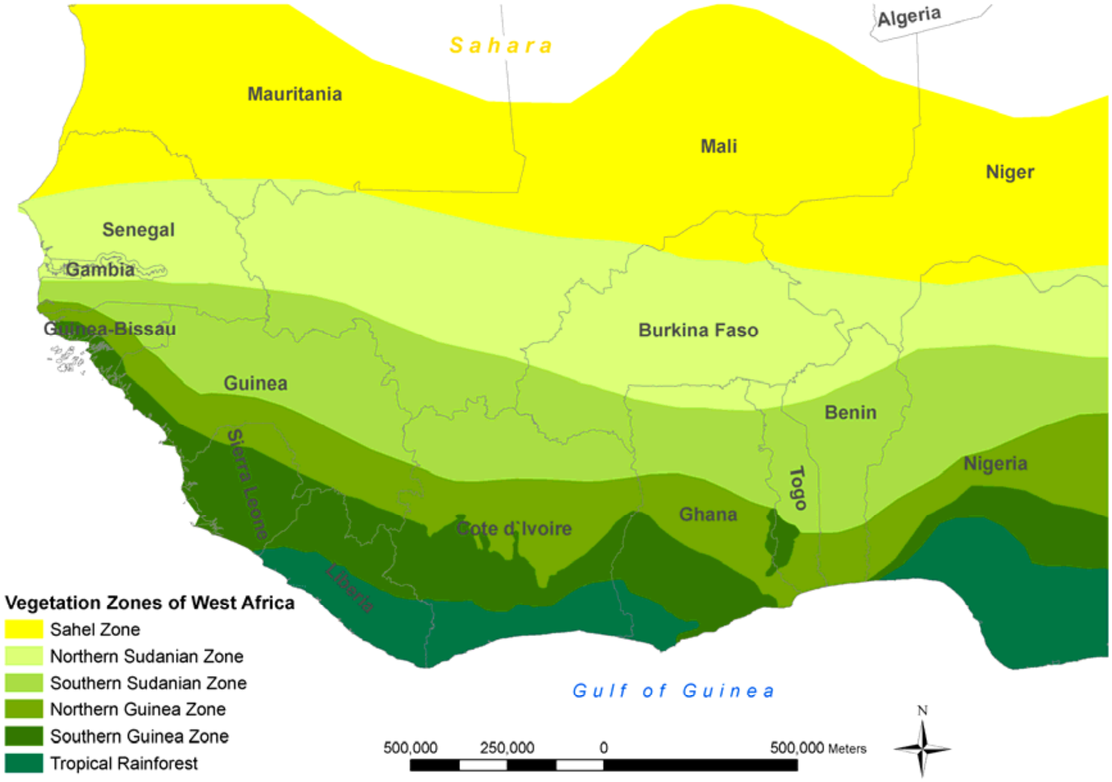

Figure 1.2-4: The vegetation zones of West Africa following White (1983). Increasing aridity from south to north leads to vegetation types with decreasing tree cover from tropical rainforests at the Gulf of Guinea to the Sahel zone at the border of the Sahara desert.

Additionally, steep local gradients of grazing pressure from protected areas to areas of intensive land-use pressure in close vicinity to settlements lead to a heterogeneous distribution of grazing pressure in a savanna landscape (Augustine, 2003; Linstädter, 2008). These specific environmental settings provide a kind of natural experimental setting to disentangle the relative importance of a diverse set of drivers in savanna ecosystems.

1.3 MAIN DRIVERS OF WEST AFRICAN SAVANNA ECOSYSTEMS

West African savanna ecosystems depend on complex interactions between (a)biotic drivers like climate, topography, soils, geomorphology, grazing by domestic and wild animals, cultivation, and fire (Backeus, 1992; Oesterheld et al., 1999) which act on hierarchically ordered scales. Climate limits the appearance of savannas on a continental to regional scale, geomorphology affects soil characteristics and water availability at a regional/landscape scale, topography determines rainfall patterns and water distribution on the landscape scale, whereas soil properties and disturbances act at local and patch scales (Coughenour & Ellis, 1993).

Abiotic drivers in savanna ecosystems

Fire is an essential characteristic of most tropical savannas (Delmas et al., 1991) caused by a distinct dry season leading to an accumulation of dry flammable plant material (Scholes & Walker, 2004). Though some fires are initiated by lightning strikes, most fires are anthropogenic and hominids started to expand and maintain savannas by use of fire around 2.5 million years ago (Brain & Sillent, 1988). Consequently, tropical savannas account for over 60% (2008) of global active fire area (Boschetti, Stehman, & Roy, 2016) but a decreasing trend can be observed in recent years due to agricultural expansion and intensification (Andela et al., 2017). In West Africa, large fires occur more often within protected areas than in surrounding regions (Gregoire & Simonetti, 2010). For instance, fire is used as a management tool in Nazinga Classified Forest (Mäkelä & Hermunen, 2007) and Mole National Park (Sackey & Hale, 2008).

Fire and grazing are alternative consumers of vegetation productivity. Grazing hinders the accumulation of fuel and can thus completely suppress fire (Kucera, 1981) or at least fire intensity is reduced by herbaceous biomass reduction and trampling by livestock (Gonzalez-Perez et al., 2004; Savadogo, Sawadogo, & Tiveau, 2007). Oesterheld et al. (1999) found most fire events occur in humid savanna areas.

Additionally, their study revealed that fire has largely positive effects in more humid areas and negative effects on the drier side of the gradient. It was also found that the timing of fire events, i.e. early “light” fires when the vegetation is still moist and late “heavy” fires on dry vegetation, is very important for the ecological consequences of fire.

Climatic aridity is an important driver of dryland rangelands and is often positively correlated with degradation (Thiombiano & Tourino-Soto, 2007). Arid areas experience high climatic variability and are thus prone to droughts as well as unusually heavy precipitation events (Oesterheld et al., 1999). Disturbances by climatic variations and grazing become particularly important at the drier boundary of the biome where they can transform grasslands into desert-like systems (Dodd, 1994), further increasing the risk of soil erosion (Thiombiano & Tourino-Soto, 2007). Aridity and frequent drought events favour an increase of annual grass species in savanna rangelands (Hempson et al., 2015), which leave the soil without a protective vegetation cover during the dry season, thus triggering degradation processes like soil erosion and soil salinization (Milton et al., 1994).

Aridity and grazing are drivers highly synergistic in their effect (Turner, 1998a) and often correlate, i.e. areas of low annual precipitation are mainly used for livestock keeping. This is due to the marginality of arid land making cropping increasingly risky, to diversify income sources and to deal with the spatial and temporal variability of production potentials (Jones & Thornton, 2009).

Biotic drivers in savanna ecosystems

The effects of the existing variety of animal production systems differ considerably for different land cover types (Phelps & Kaplan, 2017). In many parts of Africa, rangelands are mostly under communal tenure. With increasing population density, a typical transition occurs from agro-pastoral to mixed crop/livestock systems of progressive intensification (Herrero et al., 2009). At the same time, traditional institutions of communal tenure often collapse, and with them sustainable modes of natural resource management (Ostrom, 1990).

Due to West Africa's steep climate gradient with increasing aridity from the South to the North, the length of the growing seasons differs considerably between regions. This difference has tremendous implications for livestock, since animals can only gain weight during the wet season and lose weight over the dry season (Poppi & McLennan, 1995). If the growing season is too short to compensate for losses during the dry season, livestock keepers are forced into transhumance (Brottem et al., 2014) to extend the time of energy surplus.

While moderate grazing can act as an essential disturbance regime in grasslands, thereby increasing species diversity and protecting wildlife biodiversity in savanna landscapes (Maestas, Knight, & Gilgert, 2003), grazing can also promote degradation processes and a loss of ecosystem services in manifold ways (Eldridge & Delgado-Baquerizo, 2017) and livestock grazing is thus (officially) prohibited in protected areas. Still, a violation of grazing prohibitions for protected areas is often observed in West African savanna areas (Traoré et al., 2012).

In savanna ecosystems, intensive livestock grazing (**Figure 1.3-1**) can trigger the establishment of grazing-induced vegetation, e.g. grazing lawns (Archibald, 2008; Hempson et al., 2015), and shift the relative importance of drivers compared to natural systems (Oesterheld et al., 1999). Another typical vegetation response to heavy grazing in savanna ecosystems is a shift from long-lived perennials to annuals and forbs with an associated decrease in production (Fuhlendorf & Engle, 2001), but partially also an increase in forage quality (Penning de Vries & Djitèye, 1982).

An often observed selective grazing behaviour by animals influences tree density and ecosystem diversity on a broader scale (Asner et al., 2009) as well as plant age, canopy density (and thus soil moisture and light penetration), and nutrient availability at the plot level (Day and Detling 1990; Holland, Parton et al. 1992). Thus, unlike in most terrestrial ecosystems, grazing is a dominant factor determining primary production in savannas (Frank, McNaughton et al. 1998).

Figure 1.3-1: Rangeland vegetation intensively grazed by cattle in the Sudanian savanna of Upper East Region, Ghana, West Africa (photo by R. T. Guuroh).

C_4 plants are well adapted to high temperatures (Sage & Kubien, 2003) and are most common in grasslands and savannas within 40° of the Equator (Ehleringer et al., 1997). Furthermore, these arid areas are also more drought prone and growing seasons might be shortened by late-season drought events. Here C_4 plants can still be active and are more tolerant of heat stress that may accompany episodic heat events (Sage & Kubien, 2003).

1.4 THE ECOSYSTEM SERVICE OF FORAGE SUPPLY

The Millennium Ecosystem Assessment (2005) defined ecosystem services (ESs) in general as being “the benefits people obtain from ecosystems”. ESs can be further classified into provisioning services (e.g. food, water, and forage); regulating services (e.g. erosion control); cultural services (e.g. recreational areas); and supporting services (e.g. primary production).

In Sudano-Sahelian savannas, 45% of households depend on livestock income sources, and nearly half of them are facing a recent decrease in their revenue (Mertz et al., 2010). Thus forage with its two components, i.e. forage quality and quantity, is besides crop products an important provisioning ecosystem service provided by West African savannas (Leemans & de Groot, 2003). Forage supply is particularly important in the more arid zones of West Africa, where livestock production is a major feature and contributes largely towards meeting food needs, providing draught power, cash income and manure to maintain soil fertility and structure (www.fao.org). In Northern Ghana for example, forage is used by around 90% of the population and is regarded as having few or no substitutes (Boafo, Saito, & Takeuchi, 2014).

Climate change impacts on forage resources

Projections of the effect of a changing climate predict for the Sudano-Sahelian zone of West Africa a warming of the surface air temperature between three and four degrees with an additional change of daily precipitation ranging from -0.02 to +0.02 mm by the end of the 21st century (**Box 1.4-1**). The inconsistency of the rainfall projections may be related to an unclear relationship between Gulf of Guinea and Indian Ocean warming, land use change and the West African monsoon (IPCC, 2007).

The floristic composition of a savanna system is not only influenced by the total amount of precipitation but also by the intra-annual distribution of rainfall events (Lohmann et al., 2012). The effects of climate change on rangeland vegetation are generally hard to predict, since the responses of different species of grazing lands can differ greatly (Tietjen & Jeltsch, 2007) and also stimulatory effects have to be taken into consideration such as an increased ambient CO_2 level (Campbell, Stafford Smith, & GCTE Pastures and Rangelands Network members, 2000).

Box 1.4-1: Analogous climates

To ensure a meaningful determination of the research area, an analysis of **analogous climates** (**Figure 1.4-1**), i.e. areas that cover climatic situations that might be encountered at WASCAL's core research sites in 2080, is performed. This assessment is based on 19 bioclimatic variables (Hijmans et al. (2005); *www.worldclim.org*) with general relevance to ecosystems and land-use and is based on a SRES A2a scenario (special report on emissions scenarios of the intergovernmental panel on climate change (IPCC)).

The analysis indicates that in the future the climate of WASCAL's core research sites will probably be more humid than today, therefore areas to the south are added to the research area. However, climate scenarios for Africa exhibit a high degree of uncertainty (Hulme et al., 2001), especially with respect to precipitation and seasonality. Therefore, the investigation area is further extended to the north to ensure that climatic situations are captured that will possibly occur but are less likely (increasing aridity).

Figure 1.4-1: Analysis of analogous climates. The oval indicates the area of the WASCAL core research sites in Ghana, Burkina Faso and Benin in the West African Sudanian savanna. Blue areas represent regions with a climate that resembles future climate conditions in the WASCAL core research sites. Areas with lighter blue colour feature conditions more similar to future conditions in the WASCAL core research sites.

With respect to past effects of climate change on West African vegetation, there is also considerable disagreement (Heubes et al., 2011). While local studies have found that vegetation zones have shifted southwards (Wezel & Lykke, 2006; Wittig et al., 2007), long-term satellite observations do not support these findings (Tucker et al., 1991; Tucker & Nicholson, 1999), or even found a greening of West African vegetation during the past decades (Olsson, Eklundh, & Ardo, 2005), indicating higher levels of forage production.

Recent modelling approaches have shown that the prospective carrying capacity of savanna grazing systems is highly dependent on climate conditions (Lohmann et al., 2012). Since climate change will likely alter the timing and duration of the growth period, it will definitely have considerable effects on the ecosystem service of forage provision and thus on livestock production in general.

Climate change mitigation measures

In general, an adaptive rangeland management can mitigate or even compensate negative effects of climate change to a certain extent - such as a decrease in mean annual rainfall, and/or an increase in rainfall variability - on forage quality and quantity (McAllister et al., 2006).

Mobility appears to be a crucial element in adapting to rainfall variability (Martin et al., 2014), but often adaptive measures are foiled by steadily increasing demands of land (Mertz et al., 2010). In West Africa, the politically motivated trend to suppress pastoral mobility has resulted in an accumulation of animals on decreasing grazing areas with the negative consequences of overgrazing and degradation, additionally to the challenges attributed to climate change (Davidheiser & Luna, 2008).

Pasture degradation implies a reduction of pasture productivity. In West African savanna rangelands, degradation is caused by complex interactions between pasture management practices (including fire management), pasture age after farming activities, edaphic conditions and variable climate (Nacoulma et al., 2011; Savadogo et al., 2007; Savadogo et al., 2009).

Improved methods for estimating and mapping forage quality may lead to enhanced rangeland management practices through a better understanding of the optimal distribution of herbivores (Zengeya, Mutanga, & Murwira, 2012) which prevents pastures from undergoing degradation. Therefore, a fast and automated monitoring system could potentially highlight grazing lands in danger of degradation and thus mediate or monitor the implementation of adaptive land management strategies that can potentially mitigate negative effects of climate change on forage supply (Guuroh et al., 2018).

There is an urgent need to identify and implement “no-regret” measures that could not only be beneficial for the agricultural sector, but also potentially mitigate negative effects of climate change (Mertz et al., 2011). We know that different land use systems (locally evolved sets of management strategies) feature different degrees of adaptation to changing environmental conditions (Fabricius et al., 2007). Hence, spatio-temporal patterns of forage quality and quantity can also be used as indicators for the adaptive capacity and resilience of rangelands to climate change.

Potential drivers of forage supply

Spatio-temporal patterns of forage supply are complex and vary considerably in both, space and time (Hiernaux et al., 2009; Wezel & Schlecht, 2004). However, we still have a limited understanding of the individual effects of different drivers jointly shaping the provisioning ecosystem service of forage supply. Furthermore, it can be assumed that drivers of forage supply can differ when considering different spatial scales. For example in an East African savanna, the variation of biomass yield and other vegetation parameters was on a landscape scale mainly driven by gradients of rainfall and topography (Augustine, 2003), while grazing intensity was the most important driver on a local scale. It is thus mandatory to compare the influence of drivers of forage supply at fine and broad spatial scales.

Abiotic drivers of forage supply

Slopes often exert negative influences on forage supply, especially in regions characterised by medium to very high water erosion severity (Oldeman, Hakkeling, & Sombroek, 1990). Local terrain differences affect small scale water run-off rates leading to differences in water availability (Nacoulma et al., 2011) and creating more favourable growing conditions where water, eroded soil and nutrients can accumulate, i.e. at lowland positions (Pellant et al., 2000). However, despite less favourable abiotic conditions at footslope and upslope positions, e.g. lower soil moisture availability, increasing bare ground and the potential for rill formation (Pellant et al., 2005) or even lateritic crusts, these areas are often used for grazing while deep lowland soils are either too wet for grazing (wetlands) or converted to cropland (Nacoulma et al., 2011).

Soil moisture stimulates fresh plant growth and thus increases forage quality and quantity. In young plant parts, the percentage of dry matter, crude fibre, lignin, and cell wall is low, while leaf/stem ratio, percentages of CP, mineral constituents, ash and soluble carbohydrates as well as the amount of nitrogen uptake is still high, thus increasing digestibility (Crowder & Chheda, 1982).

Biotic drivers of forage supply

Forage quality is mainly modulated by phenology (Penning de Vries & Djitèye, 1982) and plant maturity (Hughes et al., 2013a), triggering the major characteristic of tropical pastures, i.e. a marked seasonal fluctuation in quantity, energy, and nutritive value (**Figure 1.4-2**) (Hughes et al., 2012).

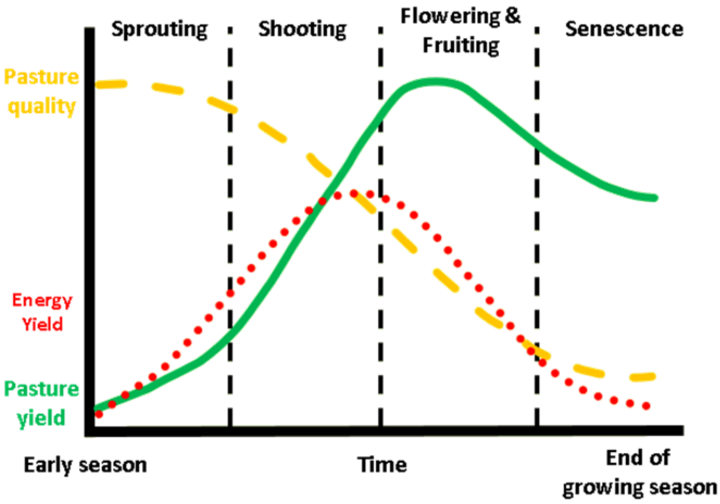

Figure 1.4-2: Changes in pasture quality (ME), (metabolisable) energy yield (MEY), and pasture yield (gBM) over the phenological development of forage plant species, adapted from *www.mla.com.au*. Pasture quality is declining right after the stage of sprouting while pasture yield reaches a maximum during the phase of flowering and fruiting. The combination of both forage parameters, MEY, peaks at the end of plant shooting.

As grasses develop from young to more mature states, there is a progressive decline in metabolisable energy (ME, **Box 1.4-2**), digestibility and crude protein (CP; e.g. to only 2% in the dry season; Atta-Krah and Reynolds (1989)) and a corresponding increase in neutral detergent fibre (NDF), acid detergent fibre (ADF; Arthington and Brown (2005)) and lignin (Laredo & Minson, 1973). However, lignification occurs only in older plants and a frequent removal of plant tissue stimulates fresh foliar regrowth (Anderson et al., 2013). Management strategies like grazing or harvesting prevent lignification of the herbaceous layer and thus improve forage quality (Hughes et al., 2013a).

The effect of seasonal fluctuations in savannas results in poor forage quality at the end of the rainy season and the whole dry season, so that available forage can hardly satisfy the nutritional requirements of livestock (Grimaud et al., 2006). In contrast, phenology increases forage quantity due to continuing plant growth over the rainy season.

Grazing can increase species diversity, e.g. by opening up the grass layer and providing many different microhabitats for annuals, pioneers, and forbs (Hahn-Hadjali, Schmidt, & Thiombiano, 2006). However, high grazing pressure can also suppress the growth of palatable forage species (Allred et al., 2012; Kgosikoma, Mojeremane, & Harvie, 2012).

Under intense grazing and sufficient nutrient availability, herbaceous vegetation can switch to grazing lawns (Hempson et al., 2015) which are very attractive for livestock compared to tall-grass swards. This is partly because of their higher leaf to stem ratio (Chaves et al., 2006) but also because lawn grasses often feature higher foliar N levels than bunch grasses (Stock, Bond, & van de Vijver, 2010). Nevertheless, plants can react to grazing in different ways, e.g. by compensatory plant growth (McNaughton, 1983) or reduced productivity due to frequent loss of tissue (e.g. Savadogo et al. (2007)).

Box 1.4-2: Metabolisable energy and the Hohenheim *in vitro* gas test

Metabolisable energy (ME) is defined as the "gross energy intake minus fecal, methane, and urinary energy" (Steiger Burgos et al., 2001). It thus corresponds to the actual energy amount of foodstuff that is available for beings. In the case of forage for ruminant species, it was observed that rumen fermentation, which is mainly affected by the amount of carbohydrates, is closely linked to gas production (Getachew et al., 1998). A well-established *in vitro* method to determine gas production by incubation of feeding stuff with rumen liquor is the **Hohenheim *in vitro* gas test** (HGT, **Figure 1.4-3**) (Menke & Steingass, 1988). A variety of different estimating equations have been developed, so that by inclusion of other chemical determinations, e.g. protein, the metabolisable energy content of forage can be determined based on gas production (Menke et al., 1979). The HGT is a superior method for the assessment of nutritional information because it can also account for microbial degradation characteristics (El Hassan et al., 2000) caused by anti-nutritional compounds, e.g. tannins, saponins or alkaloids (Getachew et al., 1998). This can be accomplished by using rumen fluid of donor animals, e.g. sheep or cows, which contains a natural spectrum of rumen microbes.

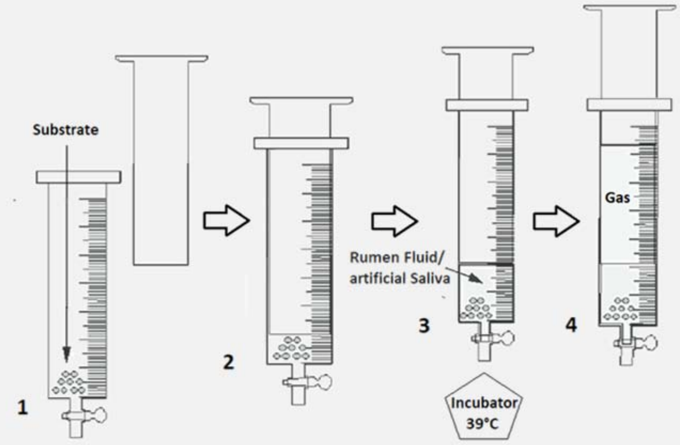

Figure 1.4-3: Procedure of the Hohenheim gas test, adapted from Pandian et al. (2016). 1) 200 mg milled feeding substrates are weighted into a syringe; 2) the plungers are greased with vaseline and used to close the syringe; 3) 30 ml of a mixture of rumen fluid and artificial saliva is added to the substrate using a disperser and subsequently the syringe is placed in an incubator with a temperature of 39°C; 4) after defined intervals of time, readings are taken of gas produced by rumen microbes. Additionally, the whole procedure has to be performed for blank (i.e. rumen fluid/artificial saliva mixture on its own) and standard feed samples to determine correction values (Menke & Steingass, 1988).

1.5 REMOTE SENSING APPLICATIONS

The expected climatic uncertainties and the associated challenges for land use in West Africa in times of rapid global change (U.S. Global Change Research Program, 2016) make it indispensable to monitor the dynamics of these economically important ecosystems. Due to the large size of grazing systems and due to the limited infrastructure, remote sensing methods are well qualified to detect land cover changes and to study human-environmental relations (Tong et al. (2017); e.g. Zimmerer (2016)). It is thus not surprising that most suggested forage monitoring approaches for the African continent make (in any manner) use of remote sensing technologies (e.g. Kaitho et al. (2007); Palmer et al. (2016); Stuth et al. (2005); Tsalyuk, Kelly, and Getz (2017)).

Introduction to remote sensing (RS)

While “remote sensing” in a general sense means the gathering of information at a distance, a more meaningful definition for the scientific method defines it as the “observation of the Earth’s land and water surfaces by means of reflected or emitted electromagnetic energy” (Campbell & Wynne, 2011) measured from handheld (ASD Inc., 2006), airborne (Green et al., 1998) or spaceborne imaging sensors (Ungar et al., 2003). Optical RS data, consisting of visible, near-infrared, and shortwave infrared bands of varying radiometric, spatial, spectral, and temporal resolutions (Shao, 2016), is the most commonly used type of data. With regard to the spectral resolution of RS data, one can distinguish multispectral data using several broad spectral regions, and hyperspectral data (**Box 1.5-1**), i.e. a high number of narrowly defined spectral channels (Campbell & Wynne, 2011).

Box 1.5-1: Hyperspectral remote sensing

Hyperspectral remote sensing allows for the acquisition of multidimensional images in hundreds of contiguous narrow spectral bands so that for each pixel a complete radiant spectrum can be derived (**Figure 1.5-1**) (Goetz et al., 1985).

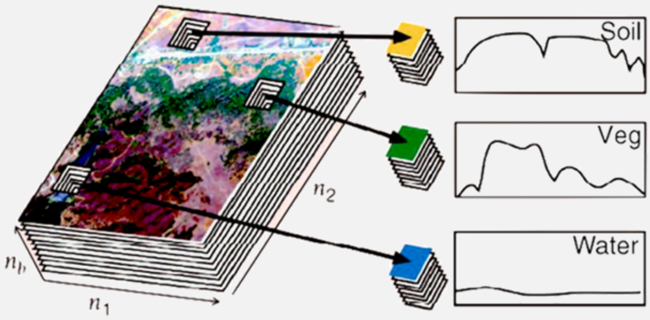

Figure 1.5-1: Composition of hyperspectral images (n_1 columns x n_2 rows) with various (n_b) narrow spectral bands whereby each pixel presents a continuous spectral curve with distinctive absorption features representative of different surface targets (the figure is an excerpt from a figure in Bioucas-Dias et al. (2013)).

These detailed spectral and spatial information enable a precise determination of surface material or estimation of physical parameters for many different fields of applications, such as ecology, geology, geomorphology, limnology, pedology, and atmospheric science (Ben-Dor et al., 2013). The full spectral range usually covers the spectral regions of VIS (visible), NIR (near infrared), SWIR (shortwave infrared), and potentially also MWIR (midwave infrared) and LWIR (longwave infrared) (**Figure 1.5-2**). Spectral curves are often quite distinctive for different surfaces due to the absorption features of the material, and many of them are already available in spectral libraries (Ben-Dor et al., 2013). This richness of spectral details represents the main advantage of hyperspectral RS in comparison to multispectral broad band systems (**Figure 1.5-3**).

However, disadvantages of hyperspectral RS are the high dimensionality, band correlation, and size of hyperspectral data, linear and nonlinear spectral mixing (Bioucas-Dias et al., 2013), as well as a lower signal-to-noise ratio due to the short dwell time of data acquisition for each pixel, atmospheric interferences of gases and aerosols and varying illumination conditions during data acquisition (Ben-Dor et al., 2013).

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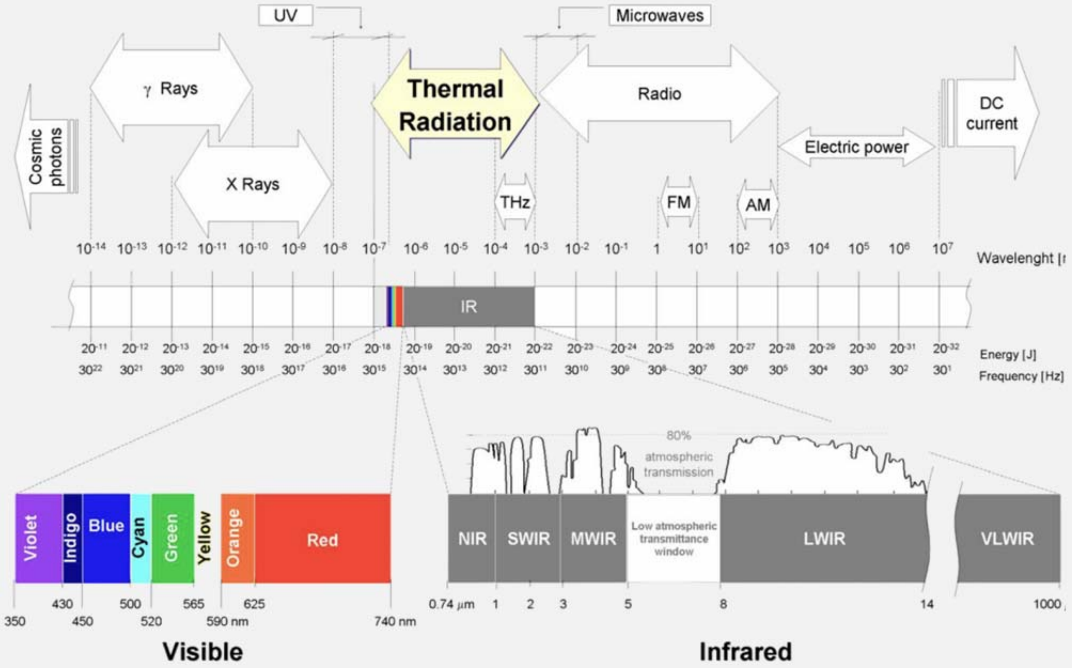

Figure 1.5-2: The electromagnetic spectrum (figure from Ibarra-Castanedo (2005)) with wavelengths (in Meter), energy (in Joule) and frequency (in Hertz) of electromagnetic radiation. The region covered by hyperspectral remote sensing has been enlarged, i.e. the visible region from 350-740 nm as well as the infrared region from 0.74-1000 µm, whereby most sensors cover only the region of near infrared (NIR) and shortwave infrared (SWIR). Note that this subdivision is somehow arbitrary and varies from one source to another. UV: ultraviolet; THz: Terahertz radiation; FM: frequency modulation; AM: amplitude modulation; IR: infrared; MWIR: midwave infrared; LWIR: longwave infrared; VLWIR: very longwave infrared.

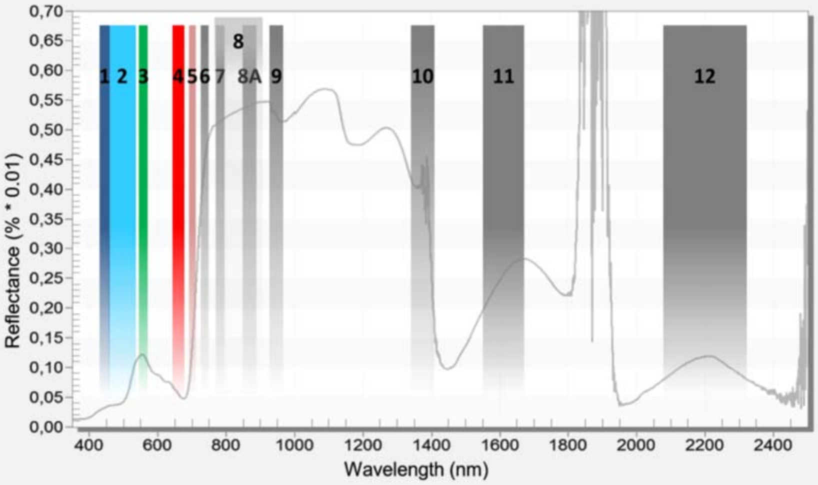

Figure 1.5-3: Simplified exemplification between a reflectance curve of vegetation from a hyperspectral system and the spectral coverage as well as the spectral resolution of a multispectral sensor (here Sentinel-2). Wavelengths around 1400 nm, 1900 nm, and over 2400 nm are highly affected by atmospheric water vapour. Sentinel-2 band 10 is used for cirrus detection (*sentinel.esa.int*).

Remote sensing for rangeland monitoring

Since its inception, RS techniques have been developed inter alia for applications on rangelands, and many indicators for rangeland health applicable for monitoring routines can thereby be directly determined in a cost-effective way (Hunt et al., 2003). Indicators of rangeland health that have been successfully extracted from RS data include the determination of rangeland productivity based on peak biomass (e.g. Mutanga & Skidmore, 2004b), time series analysis (Brüser et al., 2014), leaf area index (LAI; e.g. Qi et al. (2000)) as well as the utilisation of the Normalized Difference Vegetation Index (NDVI) to estimate ANPP (Paruelo et al., 2000). Moreover, the occurrence of noxious and/or invasive rangeland plant species, e.g. spotted knapweed and babysbreath in US rangeland (Lass et al., 2005), and mapping of vegetation formations, e.g. in relation to bush encroachment (Munyati, Shaker, & Phasha, 2011), could be done based on RS techniques. In addition, LiDAR (light detection and ranging) technology has been used to measure vegetation properties, e.g. vegetation heights, spatial patterns, and canopy cover (Ritchie et al., 1993), erosion features like dunes (Rango et al., 2000), topography (Alexander, Deak, & Heilmeier, 2016), and aerodynamic roughness (Brown & Hugenholtz, 2011). Especially hyperspectral data can be used to determine the fractional cover of photosynthetic vegetation, non-photosynthetic vegetation and bare soil coverages, e.g. in Australian savannas (Guerschman et al., 2009). SAR (synthetic aperture radar) data provides information on the water content of the vegetation (Xing, He, & Li, 2014) and the soil (Moran et al., 2000) and thermal infrared imagery is useful to distinguish bare soil from senescent vegetation (French, Schmugge, & Kustas, 2000).

Remote sensing of forage supply

Rangeland health monitoring is particularly valuable as it addresses the need to determine the amount and quality of provided forage. Since the laboratory assessment of forage characteristics is labour-intensive, costly, time-consuming and limited to sampling vegetation at a few points (Pullanagari, Kereszturi, & Yule, 2016), RS technologies are a useful addition that offer the means to map forage supply over large areas. This is of special relevance due to the patchy distribution of forage quality and quantity parameters (Knox et al., 2011). In this regard, hyperspectral remote sensing data has proven to be particularly useful (Ustin et al., 2009) due to its many narrow and continuous spectral bands that allow the detection of plant properties otherwise masked by broad multispectral bands (Mansour et al., 2012). Hyperspectral reflectance of vegetation canopies allows for the detection of characteristic absorption features resulting from the vibration and bending of molecular organic bonds (e.g. of carbon, nitrogen, hydrogen and oxygen) as well as electron transitions related to the chlorophyll concentration (Kokaly & Clark, 1999; Peterson & Hubbard, 1992; Townsend et al., 2003).

The most direct application of (hyperspectral) RS for the determination of forage quantity, e.g. herbaceous biomass (BM), is the use of a field spectroradiometer (**Box 1.5-2**). Here, the vegetation´s reflectance is measured in the field and related to a number of BM calibration samples taken from the measured plant canopy. This measurement technique, called field spectroscopy (**Box 1.5-3**), has often been applied for a cost- and time-effective estimation of grassland BM (Kawamura et al., 2008; Schweiger et al., 2015; Shen et al., 2008; Zhang et al., 2014). However, to create continuous maps, hyperspectral air-borne and space-borne sensors are more suitable and have been used for biomass mapping e.g. by Beeri et al. (2007); Fatehi et al. (2015); Homolová et al. (2014); Psomas et al. (2011). In this regard, even multispectral satellites can be successfully used for BM mapping purposes (Dube & Mutanga, 2015; Jiang et al., 2014; Mutanga & Rugege, 2006; Wessels et al., 2006).

Box 1.5-2: Fieldspectroradiometer

In this doctoral study, an ASD (now Malvern Panalytical) FieldSpec® 3 **fieldspectroradiometer** (hereafter FieldSpec, **Figure 1.5-4**) was used to measure the reflectance of different surfaces, mainly rangeland vegetation. A spectrometer, in general, is an optical instrument that can measure radiation (e.g. reflectance and transmittance; **Figure 1.5-5A**) in a particular wavelength region using detectors other than photographic film (ASD Inc., 2006). The FieldSpec is a full-range device, providing data over the entire solar spectrum from 350 nm – 2500 nm, i.e. the VIS/NIR/SWIR range (**Table 1.5-1**).

Figure 1.5-4: The ASD FieldSpec® 4 fieldspectroradiometer, the successor of the FieldSpec® 3 used in this study (*malvernpanalytical.com*). The fibre optic leads the radiation from the target of interest to the detectors inside the instrument (**Table 1.5-1**). For field measurements, the device is carried in a backpack with a pistol grip attached to the fibre optic (**Figure 1.5-5B**).

Reflectance is defined as “the ratio of energy reflected from a sample to the energy incident on the sample. Spectral Reflectance is the reflectance as a function of wavelength” (ASD Inc., 2006). To determine the reflectance of a target material, the spectral response of a reference sample (REF), e.g. a Spectralon white reference panel (**Figure 1.5-5B**), as well as of the target itself (TAR) has to be measured and calculated by dividing TAR/REF.

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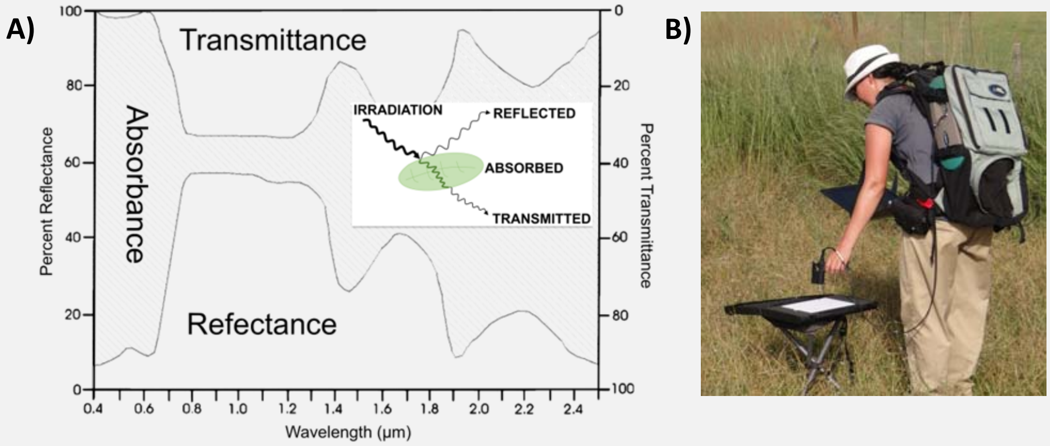

Figure 1.5-5: A) Partitioning of the vegetation's spectral response into reflectance, absorbance, and transmittance (adapted from *geol-amu.org*). B) Calibration of an ASD FieldSpec® 3 spectroradiometer using a white reference panel to measure the vegetation's spectral reflectance (photo by K. Čanak).

Table 1.5-1: Characteristics of the FieldSpec detectors (ASD Inc., 2006).

Detector	**Material**	**Wavelengths sensitivity**	**Spectral resolution**	**Sampling interval**
VNIR	Silicon	350-1000 nm	≈3 nm FWHM	1.4 nm
SWIR1	Indium Gallium Arsenide	1000 nm to 1830 nm	≈10 nm FWHM	2 nm
SWIR2	Indium Gallium Arsenide	1830 nm to 2500 nm	≈10 nm FWHM	2 nm

FWHM=Full-Width-Half-Maximum

The RS based estimation of forage quality is more complex due to the high diversity of available forage quality parameters. Using field spectroscopy, most studies concentrated on the detection of nitrogen (N), cellulose, and water (Curran, 1989; Fourty et al., 1996; Kokaly & Clark, 1999). However, there are many other potentially detectable forage quality characteristics of the vegetation, e.g. CP (Lee et al., 2011), phosphorus (P), potassium (K) (Sanches et al., 2013), ADF, NDF, ash, dietary cation-anion difference (DCAD), lignin, metabolisable energy (ME), and organic matter digestibility (OMD) (Pullanagari et al., 2012). Also, the carbon (C) concentration, chlorophyll, lignin, phenol, and tannin (Roelofsen et al., 2013) as well as the proportion of photosynthetic vegetation and biomass C:N ratio (Durante et al., 2014) could be modelled using field spectroscopy.

Box 1.5-3: Field spectroscopy and Partial Least Squares Regression

The term **field spectroscopy** refers to the measurement of hyperspectral reflectance in the field environment (Milton et al., 2009). Due to the short distance to the target, the measurement procedure needs special attention (Milton et al., 2009) and requires a basic understanding of the characteristics of electromagnetic radiation reflectance geometry to assure a correct data acquisition (**Figure 1.5-6**) (McCoy, 2005).

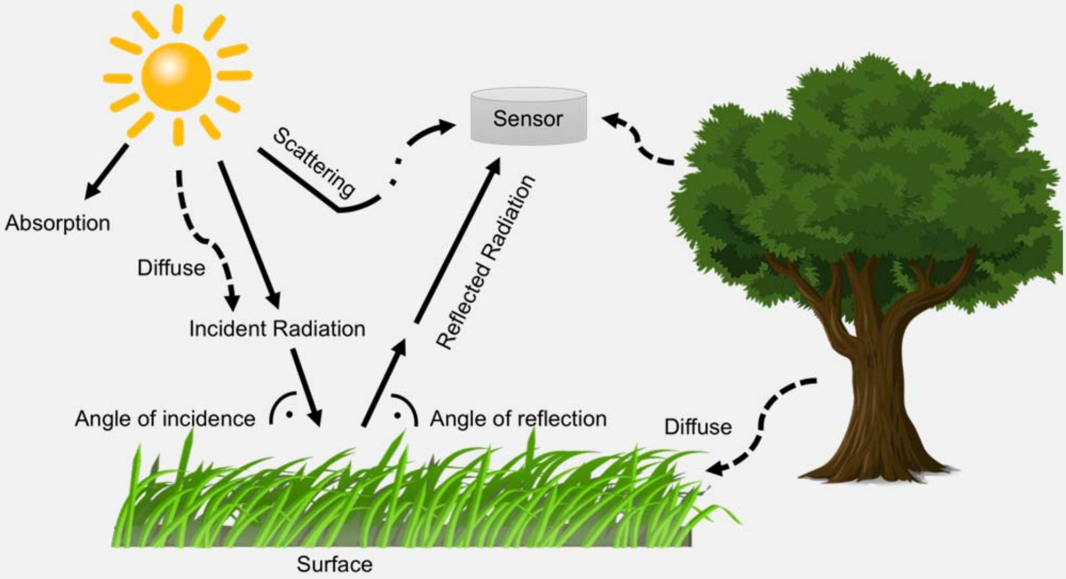

Figure 1.5-6: Basics of radiation reflectance, figure created based on graphics in (McCoy, 2005) and gsp.humboldt.edu. Sunlight can be *absorbed* by the atmosphere. *Diffuse* illumination, e.g. illumination *scattered* from nearby objects, can significantly affect the reflectance measurement at the sensor. Together with the *diffuse* light, the *direct* (not scattered) radiation represents the *incident radiation* of a surface where the *angle of incidence* equals the *angle of reflection*.

According to Milton (1987), the calibration and validation of models relating vegetation attributes to remotely-sensed data is one of the main aims of field spectroscopy. Here, a special field of research concentrates on modelling foliar chemical content from spectral reflectance. This is possible because of electron transitions in chlorophyll (0.4 - 0.7 µm) as well as the bending and stretching of e.g. the O-H bond in water and other chemicals (0.97, 1.20, 1.40, 1.94 µm) that results in specific absorption features (**Figure 1.5-7**) (Curran, 1989).

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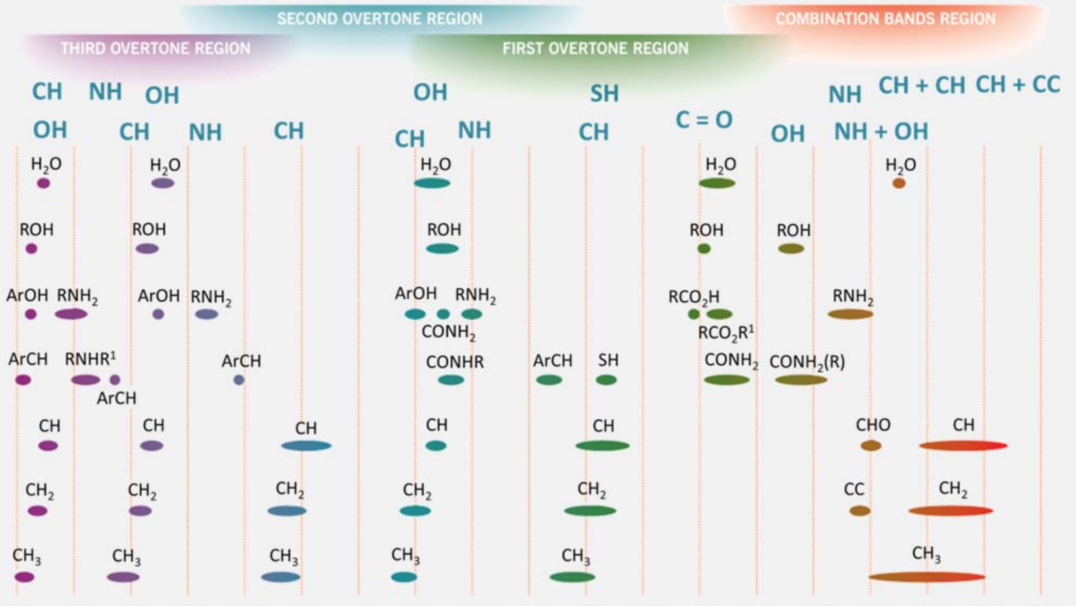

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Data sources: Ellis, J.W. (1928) Molecular Absorption Spectra of Liquids Below 3 m, Trans. Faraday Soc. 1928, 25, pp. 888-898.
Goddu, R.F and Delker, D.A. (1960) Spectra-structure correlations for the Near-Infrared region. Anal. Chem., vol. 32 no. 1, pp. 140-141.
Goddu, R.F. (1960) Near-Infrared Spectrophotometry, Advan. Anal. Chem. Instr. Vol. 1, pp. 347-424.
Kaye, W. (1954) Near-infrared Spectroscopy; I. Spectral identification and analytical applications, Spectrochimica Acta, vol. 6, pp. 257-287.
Weyer, L. and Lo, S.-C. (2002) Spectra-Structure Correlations in the Near-infrared, In Handbook of Vibrational Spectroscopy, Vol. 3, Wiley, U.K., pp. 1817-1837.
Workman, J. (2000) Handbook of Organic Compounds: NIR, IR, Raman, and UV-Vis Spectra Featuring Polymers and Surfactants, Vol. 1, Academic Press, pp. 77-197.

Figure 1.5-7: Several molecules cause absorption features in specific spectral regions that can be related to the amount of chemical constituents containing or being correlated to these molecules. Absorption features are caused by electron transitions or bond vibrations (Curran, 1989). Figure adapted from *discover.asdi.com*.

To model plant chemical constituents based on spectral reflectance data, many statistical approaches have been proposed. Here, **partial least squares regression** (PLSR) is a frequently used method in RS initially developed for NIR spectroscopy and chemometrics (Davies, 2001; Feilhauer et al., 2010). It resolves the problem of hundreds or thousands of bands often being redundant and autocorrelated. Just like principal component analysis, the data volume and dimensionality is reduced by applying a linear transformation and retaining only the significant components, i.e. latent vectors or factors, for further processing steps without loss of critical information (Harsanyi & Chang, 1994). A preferably small number of latent vectors is calculated by maximizing the information content of the spectral data but simultaneously taking into consideration the explanatory power for the dependant variable in the subsequent regression (Kooistra et al., 2001). Therefore PLSR constitutes an optimal linkage of dimensionality reduction and regression (Feilhauer et al., 2010). In this case "latent" vectors means that these factors are theoretical concepts that cannot be measured directly (Vinzi, 2010).

The use of in-situ collected vegetation spectra for the prediction of various indicators of forage quality has been found to be a time-saving, non-destructive and cost-effective alternative to laboratory analysis. However there is not much experience with the effectiveness of using spectral measurements taken in a tropical region during the rainy season. Practical restrictions pose additional difficulties to obtain interpretable data, as measurements require a cloudless sky and little water vapour in the atmosphere.

Based on hyperspectral air-borne sensors, Mutanga and Skidmore (2004a), Skidmore et al. (2010) and Mutanga and Kumar (2007) mapped N, P and polyphenols, respectively, in an African savanna using HyMap imagery. Also focusing on African savanna vegetation, Knox et al. (2011) used the CAO Alpha sensor to map N, P and fibre at the beginning of the dry season. Additionally, Beeri et al. (2007) used HyMap imagery to map the C:N ratio and CP of a mixed-grass prairie in the USA while Pullanagari et al. (2016) predicted N, P, K, sulphur, zinc, sodium, manganese, copper and magnesium in heterogeneous mixed pastures in New Zealand based on AisaFENIX hyperspectral imagery. All studies calibrated models with accuracies of $R^2 > 0.5$, except for the model predicting N in the dry season ($R^2 = 0.41$; Knox et al. (2011)).

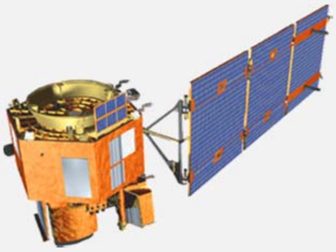
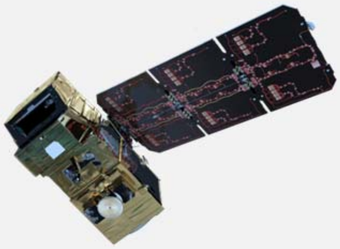
Likewise, multispectral satellite data has been successfully used for forage quality mapping purposes, e.g. WorldView-2 images for mapping the vegetation´s N concentration in Zimbabwe (Zengeya et al., 2012) and South Africa (Adjorlolo, Mutanga, & Cho, 2013; Mutanga et al., 2015), as well as RapidEye images for mapping foliar and canopy N in South Africa (Ramoelo et al., 2012). Interestingly, some of these models yielded even higher accuracies compared to the hyperspectral models predicting N (R^2 up to 0.74).

Satellite imagery offers promising tools to assess rangeland resources on local grazing land and pastures over a wide spatial and temporal range (**Box 1.5-4**). Operational tools for a satellite-based assessment of short-term dynamics in rangelands are already in service (e.g. CSIRO (2006)). However, these tools have been mainly developed for an assessment of forage quantity (and not forage quality). As both aspects are often negatively correlated (van Beest et al., 2010), they both play a crucial role in rangeland management but there is still a lack of targeted and standardized methods to assess and map the energetic value of forage resources. Remote sensing has the potential of improving our ability to map and monitor pasture degradation, to estimate biophysical characteristics of managed grasslands, and to monitor temporal and spatial patterns of ecosystem change (Numata et al., 2007). However, for making full advantage of the information content available through satellite data, a profound understanding of vegetation reflectance is needed.

Box 1.5-4: Hyperion and Sentinel-2

Hyperion and **Sentinel-2** are two potential satellite systems to map forage resources. While Hyperion is special by the fact that it provides hyperspectral images, Sentinel-2 uses cutting edge technology and was only just launched (**Table 1.5-2**).

Table 1.5-2: Comparison between Hyperion and Sentinel-2 satellite systems.

	Hyperion	**Sentinel-2**
	 Source: *www.nasa.gov*	 Source: *www.esa.int*
Mission	Earth Observing-1 (EO-1)	Sentinel mission under the Copernicus programme
Operator	National Aeronautics and Space Administration, NASA	European Space Agency, ESA
Instrument	LEWIS Hyperspectral Imaging Instrument (HSI)	Multispectral Imager (MSI)
Launch date	21.11.2000	Sentinel-2A: 23.07.2015 Sentinel-2B: 07.03.2017
Length of mission	until March 2017	minimum of seven years
Spectral coverage	hyperspectral/continuous	multispectral/discrete
Number of bands	220	13
Spectral range	400 – 2500 nm	443 nm – 2190 nm
Spectral resolution	10 nm	18 – 238 nm
Spatial resolution	30 m	10 m (bands 2:4,8) 20 m (bands 5:7,8A,11,12) 60 m (bands 1,9,10)
Swath width	7.5 km	290 km
Signal-to-noise ratio, SNR*	VNIR: 140-190, SWIR-I: 96, SWIR-II: 38	VNIR:72-174, SWIR: 50-114
Availability	freely available; mainly on order (cloud-dependant image acquisition)	freely available
Revisiting time	16 days	5 days at the equator with both satellites

*official information; actual SNR might be much lower in case of Hyperion data

1.6 GENERAL STUDY AIM

The general aim of this doctoral study is to generate a deeper understanding of the provisioning ecosystem service of forage supply in the context of global change by means of remote sensing technology. In this regard, an ease of application of developed approaches is highly desirable due to the application-oriented philosophy of the WASCAL project, which targets a provision of services to strengthen the research infrastructure and capacity in West Africa coping with climate change.

This study can be subdivided into three separate (sub-)studies that are logically connected and build on one another (**Figure 1.6-1**). The overall goal of this doctoral study in the context of the WASCAL project is research towards the establishment of an automated monitoring service providing regular maps of forage supply of West African Sudanian Savannas.

To reach this goal, the first step is to define appropriate and meaningful forage characteristics and to test whether it is possible to model these characteristics by means of direct RS techniques, i.e. field spectroscopy. The study dealing with the general tools to predict forage supply in the research area is entitled “Spectral models of forage supply”. In a second step it is necessary to deepen our contextual understanding of the underlying ecological processes and drivers of the ecosystem service of forage supply with a special focus on the implications of global change, i.e. climate change as well as land use change. This is of special relevance due to the observed and predicted climatic and anthropogenic changes within the WASCAL research area and is investigated in the study “Drivers of forage supply in savanna ecosystems”. The third and final step is the aggregation of our findings towards an application by upscaling developed models and integrating gained insights. The study “Model application for forage monitoring” presents a first attempt to upscale, map and explain variables of forage quality and quantity in space and time. It assesses the usability of two different satellite systems regarding the establishment of a regular monitoring system. In addition, drivers of forage supply on the regional scale are identified whereby our knowledge of fine-scale processes helps to contextualize our results.

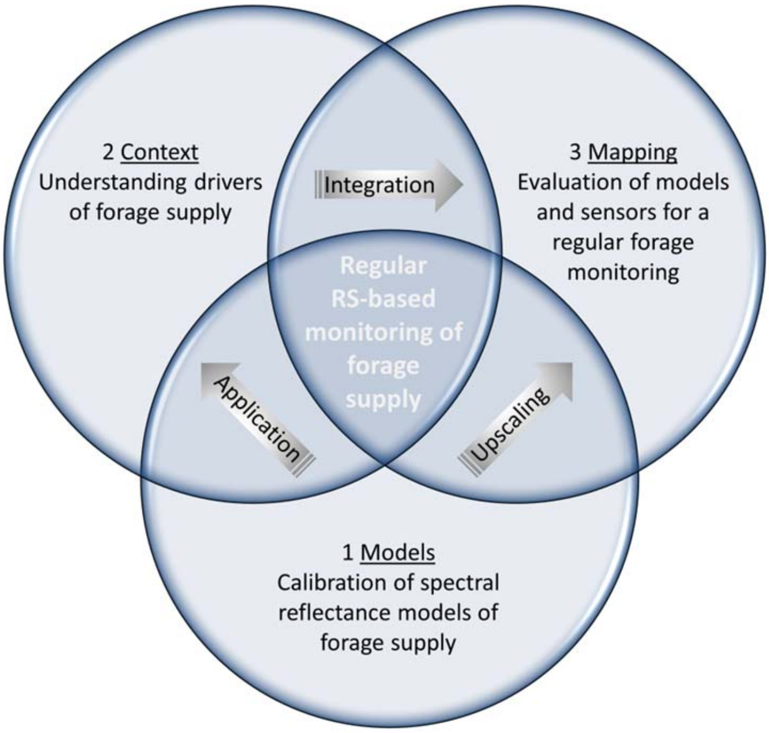


Figure 1.6-1: Symbolic sketch of the general structure of this doctoral study with the overall goal to focus research on the establishment of a regular and automated remote sensing based monitoring of forage supply. The single (sub-)studies concentrate on 1) testing appropriate tools, i.e. models, to estimate forage characteristics based on near-surface remote sensing techniques; 2) gaining a deeper contextual understanding of drivers determining forage supply; and 3) on upscaling the models from 1) and integrating the knowledge from 2) in an attempt to model, map, and understand forage supply in time and space.

Thus, the three studies presented in this doctoral thesis provide important steps towards the WASCAL objective of a climate change service, i.e. regular forage quality and quantity maps of the West African Sudanian savanna. These maps will be of great help to monitor forage supply, to better manage this valuable resource and to support pastoralists and sedentary livestock keepers in a peaceful coexistence.

I am the first author in all three studies of this dissertation described above. Here, I contributed significantly in the process of: study design, data acquisition, handling, processing, interpretation and statistical analysis, interpretation of results, manuscript writing and submission, including correspondence with editors and reviewers.

2 PUBLICATIONS OF THE DISSERTATION

2.1 SPECTRAL MODELS OF FORAGE SUPPLY

Abstract

Forage is among the essential ecosystem services provided by tropical savannas. Expected changes in climate and land use may cause a strong decline in herbaceous forage provision and thus make it advisable to monitor its dynamics. Spectroscopy offers promising tools for fast and non-destructive estimations of forage variables, yet suffers from unfavourable measurement conditions during the tropical growing period such as frequent cloud cover and high humidity. This study aims to test whether spatio-temporal information on the quality (metabolisable energy content, ME) and quantity (green biomass, BM[1]) of West African forage resources can be correlated to in situ measured reflectance data. We could establish robust and independent models via partial least squares regression, when spectra were preprocessed using second derivative transformation (ME: max. adjusted R2 in validation ($adjR^2_{VAL}$) = 0.83, min. normalised root mean square error (nRMSE) = 7.3%; BM: max. $adjR^2_{VAL}$ = 0.75, min. nRMSE = 9.4%). Reflectance data with a reduced spectral range (350-1075 nm) still rendered satisfactory accuracy. Our results confirm that a strong correlation between forage characteristics and reflectance of tropical savanna vegetation can be found. For the first time in field spectroscopy studies, forage quality is modelled as ME content based on 24-h in vitro gas production in the Hohenheim gas test system and crude protein concentration of BM. Established spectral models could help to monitor forage provision in space and time, which is of great importance for an adaptive livestock management.

This chapter has been published as:

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[1] Here, in contrast to the other chapters, the abbreviation BM (not gBM) stands for green biomass. The naming complies with the published paper.

Introduction

Forage is among the most important ecosystem services provided by tropical savannas (Safriel & Adeel, 2005). In West Africa's Sudanian-Sahelian savannas, 45% of households depend on livestock-related income sources (Mertz et al., 2010). Forage provision has two main components: forage quantity (yield) and forage quality, i.e. its nutritional value for livestock (Beeri et al., 2007). Both components are mainly dependent on the rangeland's floristic composition, but modulated by its phenological stage and by the rainfall of a given year (Anderson et al., 2007; Pavlu et al., 2006). Floristic composition of savanna rangelands is interactively driven by environmental conditions including climatic aridity, topography, and grazing (Augustine & McNaughton, 2006; Linstädter, 2008). As West Africa has a high spatio-temporal variability in these factors (Nacoulma et al., 2011; Wittig et al., 2007), related patterns of forage provision are complex (Brottem et al., 2014; Hiernaux et al., 2009). This may have important consequences for livestock nutrition and livelihood security (Martin et al., 2014), particularly in areas where overgrazing has led to degradation (Ruppert et al., 2012a). In this context, reliable data on forage quantity and quality patterns are needed to support adaptive management strategies (Beeri et al., 2007). Since climate plays a crucial role for both forage characteristics, climate change may exert a strong influence on them (Grant et al., 2014; Ruppert et al., 2015). Consequently, monitoring and early-warning systems will gain importance to support mitigation and adaptation measures. Again, reliable data on forage characteristics are essential for such applications (Stuth et al., 2005).

Canopy reflectance as a proxy for forage properties is an easily accessible source of information. Provided a strong correlation between target variables and reflectance is found, regression models can be directly scaled up through remote sensing for tracing changes of forage provision in space and time. *In situ* collected vegetation spectra have been found to be a time-saving, non-destructive and cost-effective alternative to laboratory analysis (Curran, 1989). The approach has been successfully applied in various biomes, including temperate grasslands (Biewer, Fricke, & Wachendorf, 2009b; Kawamura et al., 2009; Sanches et al., 2013) and subtropical grasslands (Knox et al., 2011; Knox et al., 2012).

Several chemical constituents have been used as proxies to determine the quality of grazed and browsed plant material. Most of these studies focused on nitrogen (e.g. Knox et al. (2012); Sanches et al. (2013)), as this is the main constituent of crude protein (e.g. Pullanagari et al. (2012); Thulin et al. (2012)). Phosphorus is an important macro element in animal nutrition (Reid et al., 2015) and has therefore been investigated by several authors (e.g. Albayrak, Basayigit, and Türk (2011); Kawamura et al. (2009)). Apart from nitrogen and phosphorus, Mutanga, Skidmore, and Prins (2004) used *in situ* measured hyperspectral reflectance data to model potassium, calcium and magnesium concentrations. Low potassium concentrations may limit plant growth and thus, forage availability, whereas calcium and magnesium may limit voluntary feed intake, and consequently, performance, by grazing ruminants if not consumed in sufficient quantities (reviewed by Minson (1990)).

However, these are indirect proxies of forage quality with a limited potential to derive implications for animal nutrition (van Soest, 1994). To overcome these caveats, a promising approach is to combine *in vitro* assessments of forage digestibility with crude protein concentration (Menke et al., 1979). The resulting proxy of metabolisable energy (ME) is superior to other indices, as it directly quantifies forage quality as differences in digestibility (Getachew et al., 1998). It is thus surprising that field spectroscopy has up to now rarely used these proxies to evaluate forage quality. Only Hughes et al. (2014) used a comparable *in vitro* technique for the determination of ruminal organic matter digestibility and linked it to chlorophyll indices measured by a hand-held chlorophyll gun.

To ensure that robust calibration models could be built for a certain biome or vegetation zone, it is recommended to sample reflectance data over a wide range of vegetation types and over an entire growth period (Feilhauer & Schmidtlein, 2011; Marten, Shenk, & Barton, 1989). However, previous comparable studies in the tropics and subtropics only sampled along rather short environmental gradients (spanning max. 30 km with climate assumed as being constant; Skidmore et al. (2010)), and rarely over different phenological stages (e.g. Biewer, Fricke, and Wachendorf (2009a); Biewer et al. (2009b); Laba et al. (2005); Sanches et al. (2013) in temperate climates). In contrast, our study covers almost the entire climatic gradient of West Africa’s Sudanian savannas (more than 500 km), as well as a broad range of edaphic conditions and vegetation types. It thus has the potential to realistically represent forage characteristics of West Africa’s Sudanian savannas.

Although it is highly desirable to establish spectral indicators of forage quality in tropical regions, several factors make it particularly difficult to assess forage characteristics via field spectroscopy. First, a green, preferably closed herbaceous layer is mandatory to prevent interference from soil reflectance (Huete, Jackson, & Post, 1985), but can – if at all – only be found during the rainy season, with the exception of wetlands (Vrieling, de Leeuw, & Said, 2013). Second, a cloudless sky with little water vapour in the atmosphere is desirable (Hayward & Oguntoyinbo, 1987).

However, during the rainy season the weather of the study area is characterized by high atmospheric humidity coupled with frequent cloud cover (Gessner et al., 2013). For these reasons there has been little experience with field spectroscopy in tropical environments. In our study we explore several methodological approaches to address these difficult measurement conditions, including derivative analysis. Although it is known in general that derivative analysis is able to enhance information extraction from hyperspectral data (Knox et al., 2010), it has not yet been tested to specifically overcome the difficult measurement conditions of a tropical environment.

As visible and near-infrared (VNIR) spectra have a close relationship with plants' biochemical characteristics (Pullanagari et al., 2012), it might be feasible to reduce the spectral range to these bands which would allow for using smaller and more affordable VNIR field spectrometers in future studies. Until now, however, the feasibility of this half-range approach to model BM and ME of tropical vegetation has not been tested.

Our study aims at evaluating the feasibility of canopy-scale spectroscopy by correlating forage quantity and quality variables to reflectance of tropical rangelands. For this purpose, we (1) identify reflectance features and (2) evaluate methods that might enhance our ability to assess forage characteristics under tropical measurement conditions. In addition, we (3) test the feasibility of reducing the spectral range to the VNIR spectrum.

Materials and Methods

Study area

The study area covers ca. 530 x 200 km, and reaches from central Ghana to northern Burkina Faso. It comprises a steep gradient of climatic aridity. The climate is tropical, with a rainy season from May to August in the semi-arid north, and April to October in the humid south-east (**Figure 2.1-1**).

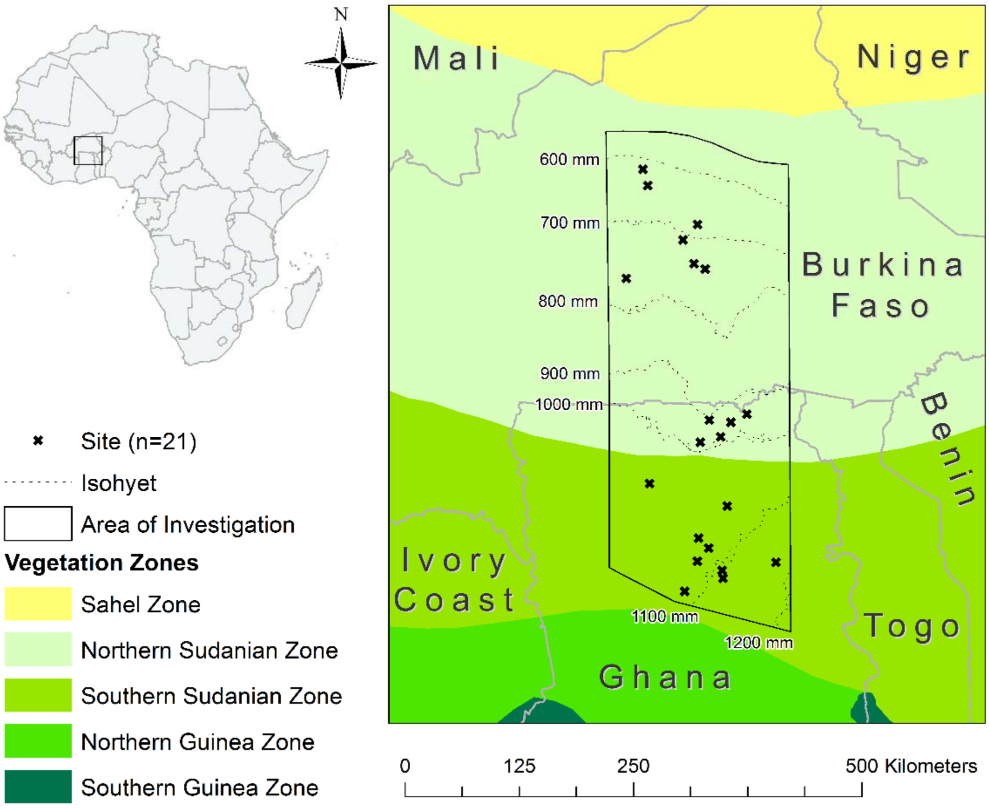

Figure 2.1-1: Map of study area and sites. Vegetation zones follow White (1983). The steep gradient of climatic aridity in the study area is indicated by isohyets of mean annual precipitation.

Geology is mainly determined by migmatite in the north and sandstone in the south. Landforms consist of small rocky elevations surrounded by sedimentary basins (Butt & Bristow, 2013).

Study design and spectral reflectance measurements

As recommended by Feilhauer and Schmidtlein (2011) and Marten et al. (1989), reflectance data were sampled over a wide range of vegetation types and over different phenological stages. Hence, sampling sites were spread along the north-south gradient. The research area was roughly divided into three zones of different precipitation regimes (high: mean annual precipitation (MAP) > 1000 mm; intermediate: MAP 800-1000 mm: low: MAP < 800 mm; see **Figure 2.1-1**) to assure a spatial spread of sampling zones. Furthermore, we used a geological map to place sites within major geological units, and a geomorphological map to select sites with an undulating landform. At study sites, we applied a stratified random sampling approach (stratified by topographic position; Table 2.1-1). Due to a heterogeneous distribution of grazing pressure in a savanna landscape (Linstädter et al., 2014), the sampling design also (non-explicitly) covered different levels of grazing pressure.

Table 2.1-1: Number of samples analysed for metabolisable energy (ME) and green biomass (BM) per precipitation zone and slope position (lowland, footslope or upslope).

Precipitation zone	**ME**			**BM**		
	Lowland	**Footslope**	**Upslope**	**Lowland**	**Footslope**	**Upslope**
High	11	15	11	10	14	9
Intermediate	19	4	4	19	4	4
Low	22	4	11	24	6	15

Data were collected during the 2012 rainy season. Measurements were performed with a FieldSpec 3 Hi-Res Portable Spectroradiometer (ASD Inc., Boulder, CO, USA) which detects light in a spectral range from 350 – 2500 nm, recorded by three separate sensors (VNIR, SWIR 1, SWIR 2). The spectral resolution of the instrument is 3 nm (FWHM) at 700 nm and 10 nm (FWHM) at 1400 nm and 2100 nm, respectively but was interpolated to 1 nm resolution (ASD Inc., 2006). Altogether, 129 plots were sampled on 21 sites (**Figure 2.1-1**). Several samples could not be used for model calibration due to partial sample losses and measurement errors in the lab. This reduced the number of samples to 101 (metabolisable energy, ME) and 105 (green biomass, BM).

Prior to each measurement, a calibration to current light conditions and a reference to reflectance were done using a Zenith alucore reflectance target. Measurements were taken at ca. 1.30 m above canopy, and thus for an area of ca. 0.25 m^2 (hereafter “plot”). The device was set to an internal averaging of fifty single measurements into one reflectance curve. For variance testing, we collected five individual measurements per plot.

Assessment of standing herbaceous green biomass and its forage quality

After spectral measurements, the plot area was clipped to stubble height (ca. 1 cm). Plant samples were air-dried and shipped to the laboratory of the Institute of Animal Science, University of Bonn (Germany). Samples were oven-dried (60°C, > 48 h) to obtain standing BM which equals green BM since only predominantly green plots were sampled. Dried samples were ground to pass a 1-mm screen size (Retsch SM1; Retsch, Haan, Germany) for analysis of *in vitro* gas production (GP) using the Hohenheim gas test (HGT; Menke and Steingass (1988)). Crude protein (CP) content was determined by LUFA NRW (Münster, Germany) using Kjeldahl´s method (method 4.1.1; VDLUFA (2012)). The ME was calculated using equation 16e by Menke and Steingass (1988):

ME (MJ kg^{-1} dry matter, DM) = $2.20 + 0.1357\ GP + 0.0057\ CP + 0.0002859\ CP^2$, where GP is expressed as ml 200 mg^{-1} DM and CP is expressed as g kg^{-1} DM.

Regression models for forage characteristics

To address the characteristic instability of atmospheric conditions during the rainy season of tropical savannas (Hayward & Oguntoyinbo, 1987), we used only spectral measurements showing consistent reflectance curves. In this way, outliers and measurements taken under shifting atmospheric conditions were omitted. Remaining measurements were averaged to obtain single per-plot reflectance spectra.

For model calibration, spectra were smoothed using a Savitzky-Golay filter (Savitzky & Golay, 1964). To account for different levels of noise in the spectra, individual filter adjustments were used (**Table 2.1-2**). The signal-to-noise ratio was increased via adjusted filter sizes to reduce noise (SWIR region) but preserving important spectral features (NIR region). To avoid artefacts in the spectral curve, jump points were placed in noisy regions of strong interference with atmospheric gases which were excluded from consecutive analyses.

Table 2.1-2: Adjustments of the Savitzky-Golay filter used to smooth spectral data showing varying levels of noise over the spectral range.

Spectral range [nm]	Polynomial degree	Window size
350 to 1350	5	45
1351 to 1850	5	61
1851 to 2400	5	111

A partial least-squares regression (PLSR; Wold, Sjöström, and Eriksson (2001)) was used to model the relations between spectral data and target variables (ME and BM). Similar to principal component analysis, PLSR reduces the volume and dimensionality of spectral data by applying a linear transformation to identify a small number of “latent” vectors (Vinzi, 2010). It aims to retain only significant components with a high explanatory power in subsequent regression (Harsanyi & Chang, 1994). PLSR is a good choice when the number of explanatory variables (i.e. spectral bands) is greater than the number of observations (Wold et al., 2001), which is the case in our study.

We used the PLSR implementation in the R package “autopls” (Schmidtlein, Feilhauer, & Bruelheide, 2012), which provides an automated backward selection of bands. The filtering rule in the iterative feature selection was based on significance in jackknifing. The proportion of removed independent variables per iteration (10% or 25%) was determined by model improvement in validation. During PLSR, we also performed multiplicative scatter correction (Martens & Naes, 1992) and brightness normalization of reflectance spectra (Feilhauer et al., 2010).

Model validation was based on two approaches. First, an adapted cross-validation was performed by successively excluding all plots pertaining to one of the 21 sites. This method (“leave-one-site-out”, losoCV, as implemented in the R package “autopls”), mitigates the effects of spatial autocorrelation. Second, a one hundred times repeated cross-validation was done by excluding randomly 25% of all data points. To evaluate model fit, we calculated normalized root mean square error (nRMSE) in validation.

Reduction of spectral range

To evaluate the suitability of a reduced spectral range, spectra taken with the full-range spectroradiometer were cut to half-range (350 – 1075 nm), and separate models were calibrated with the same methodology as for full spectra. This allowed a direct comparison of models based on the two spectral ranges.

Spectral preprocessing

To test whether preprocessing techniques could increase the accuracy of regression models under tropical measurement conditions, first and second derivative calculations were applied (Laba et al., 2005; Thulin et al., 2012). In this study, a commonly used approximation of the derivative spectrum was attained by calculating the differences between all consecutive values of the spectrum.

Results

Reflectance as a proxy of forage characteristics

For the two proxies of forage quality and quantity, a broad range of values was sampled. Values for ME ranged from 4.6 to 17.2 MJ kg^{-1} DM (median: 9.1 MJ kg^{-1} DM), values for BM from 33.9 to 1336.6 g m^{-2} (median: 205.08 g m^{-2}). In the case of BM, data was log-transformed to obtain a normally distributed data set.

For ME and BM, moderate PLSR model fittings were achieved with full-range and half-range spectra using unprocessed spectra (Table 2.1-3).

Table 2.1-3: Summary of model fittings for forage characteristics using partial least-square regression. High $_{adj}R^2$ values and low nRMSE values indicate a good fit of the regression models. For model calibration, full-range (Full) and half-range (Half) spectra were used, respectively. Model validation was done via leave-one-site-out (VAL_{LOSO}) and repeated cross validation (VAL_{CV}).

Model	**$_{adj}R^2$**	**$_{adj}R^2$**	**nRMSE [%]**	**nRMSE [%]**
	VAL_{LOSO}	**VAL_{CV}**	**VAL_{LOSO}**	**VAL_{CV}**
ME_{Full}	0.56	0.55	11.7	11.8
ME_{Half}	0.43	0.47	13.2	12.8
BM_{Full}	0.64	0.66	11.3	11.1
BM_{Half}	0.66	0.64	11.0	11.4

Values of $_{adj}R^2$ were clearly lower (0.08 - 0.23) for the two models for forage quality (ME_{Full}, ME_{Half}) compared to the two models for forage quantity (BM_{Full}, BM_{Half}) which reached values up to 0.66. Similarly, relative errors for BM_{Full} and BM_{Half} (ca. 11.2%) were lower than for ME_{Full} and ME_{Half} (around 11.7 and 13%, respectively), indicating less residual variance. For ME models, model fit decreased when the spectral range was reduced, while the two models for BM performed equally well ($BM_{Full\ and\ BMHalf}$; see Table 2.1-3).

To quantify the variance in reflectance that explains ME and BM, we calculated correlations between fitted ME and measured BM and vice versa (**Table 2.1-4**). Results revealed that no model was directly positively influenced by the other forage characteristic.

Table 2.1-4: Correlation of fitted ME and BM values with observed BM and ME values, respectively, revealed that no model was directly positively influenced by the other forage characteristic.

Fitted	Observed	r	*P*-value
$\mathbf{ME_{Full}}$	BM	-0.32	0.0016
$\mathbf{ME_{Half}}$	BM	-0.36	0.0003
$\mathbf{BM_{Full}}$	ME	-0.1	0.3562
$\mathbf{BM_{Half}}$	ME	-0.12	0.2336

Independent variables selected during backward selection were often related to known spectral features of relevant plant constituents. We checked this congruence for the models ME_{Full} (32 independent variables) and BM_{Full} (37 independent variables, **Figure 2.1-2**). Variables were often selected from the VNIR region whereby for the model for ME a large number of highly significant variables appeared in the SWIR between 2000 and 2300 nm.

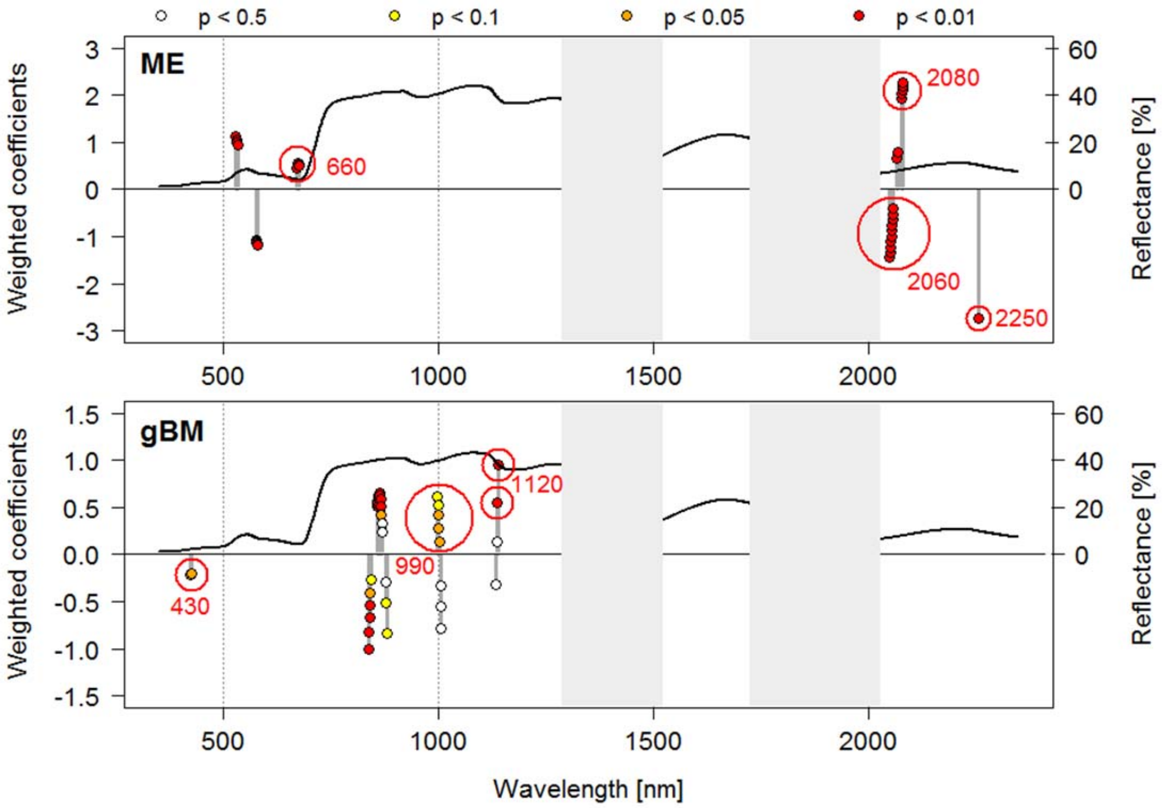

Figure 2.1-2: Regression coefficients of variables selected during PLSR backward selection for the models for ME and BM. Levels of significance are indicated by different colours. The image is overlaid by the mean spectrum. Highly significant variables that fall into regions of known absorption features (Curran, 1989) are labelled (see **Table 2.1-5**).

Table 2.1-5: Spectral regions of highly significant independent variables in the model and their functional link to absorption features of foliar chemicals (according to Curran (1989)).

Target variable	Wavelength [nm]	Associated chemical(s)	Electron transition or bond vibration
BM	430	Chlorophyll a	Electron transition
ME	660	Chlorophyll a	Electron transition
BM	990	Starch	O-H stretch, 2nd overtone
BM	1120	Lignin	C-H stretch, 2nd overtone
ME	2060	Protein, Nitrogen	N=H bend, 2nd overtone/ N=H bend/N-H stretch
ME	2080	Sugar, Starch	O-H stretch/O-H deformation
ME	2250	Starch	O-H stretch, O-H deformation

Many significant spectral bands selected for model calibration can be linked to known absorption features of foliar chemicals. These absorption features are related to chlorophyll and protein, but more prominently to energy-yielding compounds like starch, sugar and cell-wall carbohydrates (cellulose, hemicelluloses) as well as structural elements like lignin.

Effects of preprocessing techniques on model performance

In most cases model fits could be improved by applying preprocessing techniques to spectral data (Table 2.1-6; models with the lowest nRMSE are underlined).

Table 2.1-6: Model fittings for the regression of ME and BM on full-range (Full) and half-range (Half) spectral data using first (D1) and second (D2) derivative transformation, respectively. Validation was done via leave-one-site-out (VAL_{LOSO}) and repeated cross validation (VAL_{CV}).

Model	**$_{adj}R^2$**	**$_{adj}R^2$**	**nRMSE [%]**	**nRMSE [%]**	**Model**	**$_{adj}R^2$**	**$_{adj}R^2$**	**nRMSE [%]**	**nRMSE [%]**
	VAL_{LOSO}	**VAL_{CV}**	**VAL_{LOSO}**	**VAL_{CV}**		**VAL_{LOSO}**	**VAL_{CV}**	**VAL_{LOSO}**	**VAL_{CV}**
ME_{Full}-D1	0.66	0.65	10.2	10.4	**BM_{Full}-D1**	0.60	0.62	11.9	11.7
ME_{Half}-D1	0.48	0.49	12.7	12.5	**BM_{Half}-D1**	0.60	0.61	11.9	11.9
ME_{Full}-D2	0.83	0.83	7.3	7.3	**BM_{Full}-D2**	0.75	0.75	9.4	9.4
ME_{Half}-D2	0.65	0.64	10.4	10.5	**BM_{Half}-D2**	0.70	0.70	10.3	10.4

Best model fittings were attained through second derivative calculation and full-range data for both forage characteristics (ME_{Full}-D2 and BM_{Full}-D2). These models featured $_{adj}R^2$ values up to 0.83 (ME) and 0.75 (BM), while nRMSE values dropped to only 7.3% (ME) and 9.4% (BM). Applying second derivative calculation also resulted in the lowest nRMSE values for the BM and ME models using a reduced spectral range (BM_{Half}-D2, ME_{Half}-D2). Model validations were stable, since differences between VAL_{LOSO} and VAL_{CV} values were generally small (0.1 – 0.4%).

Discussion

We obtained good fits for models of forage quality (metabolisable energy, ME) and quantity (aboveground green biomass, BM) using second derivative reflectance detected with field spectroscopy. This opens up new perspectives for a prospective use of remote sensing in rangeland management and monitoring and points to alternatives for a fast and affordable detection of rangeland conditions.

Reflectance as a proxy of forage properties

Field spectroscopy studies typically rely on chemical constituents of plants as proxies for forage quality, such as nitrogen (Starks, Zhao, & Brown, 2008), CP (Biewer et al., 2009b), and phosphorus (Mutanga et al., 2004). Although these proxies may be useful to evaluate certain aspects of forage quality, they do not give a direct estimate of nutritive value for livestock (van Soest, 1994). To overcome these caveats, we directly quantified forage quality as ME, based on laboratory analyses of HGT (Menke & Steingass, 1988) and CP. Since rumen fermentation is closely linked to carbon dioxide and methane production (Getachew et al., 1998), the HGT in combination with CP is a more accurate method for assessing nutritional information, at the same time accounting for rumen microbial degradation characteristics (El Hassan et al., 2000) caused by anti-nutritional compounds (Getachew et al., 1998).

In contrast, the few studies that have previously linked ME to *in situ* measured reflectance spectra relied on near-infrared (NIR) spectroscopy to model ME of dried plant material, e.g. for grassland (Biewer et al., 2009b; Perbandt, Fricke, & Wachendorf, 2010; Pullanagari et al., 2012) and maize biomass (Perbandt, Fricke, & Wachendorf, 2011). However, relating forage variables estimated by NIR spectroscopy to field spectroscopy may obviously imply a circular reasoning. Hence, our study is the first to establish calibration models between spectral data measured in the field and ME measurements based on wet chemical analysis.

The ME showed strong correlations with wavelengths that can be related to starch and protein contents in plant material (cf. **Figure 2.1-2**, **Table 2.1-5**). These associations conform to expectations, since gas production in the rumen and, likewise, in an *in vitro* system resembling the rumen conditions such as HGT, is mainly affected by the fermentation of carbohydrates (Getachew et al., 1998) while CP strongly contributes to a high energy content of forage. In comparison, high correlations between BM and spectral bands can mainly be related to adsorption features of chlorophyll and of structural components like lignin. It is necessary to clarify that the vegetation´s BM and ME values are not directly correlated to spectral reflectance but the concentration of organic compounds is correlated to known adsorption features within the spectrum (Curran, 1989).

Several spectral regions selected by PLSR have also been selected in other studies, e.g. 655 nm, 2085 nm (Pullanagari et al., 2012) and 2084 nm (Biewer et al., 2009b) for the ME model and 990 nm and 1116 nm for the BM model (Biewer et al., 2009a). This further underlines the purposeful selection of spectral indicators during PLSR.

The negative correlation between fitted and observed forage variables (**Table 2.1-4**) agrees with previous observations of rangelands' decreasing forage quality with increasing biomass (Moreno García et al., 2014), and underlines the independence of both models.

Robustness and transferability of models

We aimed to establish robust and transferable regression models for forage characteristics of pastures situated in West Africa's tropical Sudanian savannas. For this purpose, calibration data should ideally include all possibly occurring states of the target variable (Thulin et al., 2012).

As forage characteristics in a given year mainly depend on a pasture's floristic composition (which is basically driven by climate, topography and grazing) and on its phenological stage (Anderson et al., 2007; Holmes et al., 1987), study sites covered almost the entire climatic gradient of the Sudanian zone, and measurements were spread over local gradients of grazing and topography. As we also sampled over an entire growth period, our data set comprised a wide range of vegetation types and states of Sudanian savannas.

Our study design successfully captured a broad range (difference between maximum and minimum value) of forage characteristics, i.e. 12.62 MJ kg^{-1} DM for ME and 1302.68 g m^{-2} for BM. For ME values, this can be partly attributed to one plot showing an uncommonly high CP content of 18.4%. However, this value (and hence the derived ME) still represents a plausible value for tropical grasses (Minson, 1990).

Comparable studies mostly featured lower biomass ranges, e.g. 331.6 g m^{-2} (Zhang et al., 2014) and 721.3 g m^{-2} (Kawamura et al., 2008). Zhang et al. (2014) also sampled a climate gradient in Inner Mongolia over different land use intensities. However, while they captured a range of MAP varying between 150 mm and 400 mm, our study captured a range of 600 mm to 1200 mm corresponding to UNEP aridity indices (Middleton & Thomas, 1997) of 0.31 (semi-arid) to 0.69 (humid). Although the achieved high variability of forage variables is prerequisite for the calculation of robust models, it inevitably hampered model accuracy, since different spectral signatures may have been connected to the same forage characteristic. Many studies (e.g. Biewer et al. (2009a); Mutanga et al. (2004); Serrano, Penuelas, and Ustin (2002)) have found that splitting the dataset into more homogenous subsets increased model performance. However, since our primary goal was to calibrate robust models we refrained from separating the dataset into subsets.

Methods to address difficult measurement conditions

In tropical biomes such as West Africa’s Sudanian savannas, it is particularly difficult to assess forage characteristics via field spectroscopy due to variations in surface irradiance caused by varying cloud cover (Fensholt, Sandholt, & Rasmussen, 2004; Gessner et al., 2013), and due to inferences from soil reflectance (Okin et al., 2001) caused by low vegetation cover (Bationo & Buerkert, 2001). We successfully addressed these problems by several methodological approaches.

First, we tested first and second derivative calculation, as this preprocessing technique can be crucial for the success of hyperspectral imaging approaches under difficult measurement conditions (Thulin et al., 2012). We found that model performances could be considerably improved when using second derivative spectra for model calibration. This could be explained by the fact that derivative analysis can suppress interference from soil background reflectance (Demetriades-Shah, Steven, & Clark, 1990), because the second derivative of soil spectra is close to zero. Additionally, Tsai and Philpot (1998) showed that second-order or higher derivatives are hardly influenced by illumination intensity. Hence derivative calculation also helped to standardize spectral measurements taken under varying illumination conditions. Thus derivative calculation was crucial for enabling field spectroscopy under difficult measurement conditions. Additionally, continuum removal (Mutanga et al., 2005) and logarithm of reciprocal reflectance (LOG1/R; Thulin et al. (2012)) were tested to enhance information extraction but did not perform better than derivative transformation (data not presented).

Two other techniques contributed to model improvement. As derivative calculation may intensify high-frequency noise, we implemented a filtering scheme adapted to differing noise levels over the spectral range. To address the problem that PLSR usually select a comparatively high number of independent variables, we removed insignificant variables using backward selection. Although these methods greatly improved model fits, models may still be weakened by the high variability of illumination.

Effects of reduced spectral range

Half-range models often had a lower accuracy than full-range models, but still rendered satisfactory results. This corroborates findings from studies with a comparable reduction of spectral coverage (Asner et al., 2011; Biewer et al., 2009a, 2009b). The decreased performance of half-range models could be explained by the fact that (especially for ME) significant variables were, as in other studies (Numata et al., 2007), located in the rear NIR and SWIR region, and thus outside of the half-range spectrum. Consequently, based on the results of our simulations we expect that it is possible to find good regression models for BM while for ME it is most likely that regression fit will decrease when a half-range spectrometer is used. Depending on the priorities of a study, VNIR field spectrometers will be a suitable and cost-effective alternative to full-range spectrometers. However, simulating the spectral ranges of spaceborne imaging spectrometers or multispectral satellites such as Sentinel was beyond the scope of this study.

Conclusion

Expected climatic uncertainties and associated challenges for rangelands in West Africa make it advisable to monitor the dynamics of forage provision within these ecosystems. Spectroscopy offers promising tools to achieve this objective but suffers from frequent cloud cover, high humidity, and sparse vegetation cover. By using derivative spectra and methods to improve model robustness it could be shown that spectral data can be successfully linked to variables of forage quality and quantity in tropical grasslands despite unfavourable measurement conditions.

To our knowledge, forage quality as the ME content determined by HGT and CP has never been modelled in hyperspectral studies. It is an innovative method, since it is able to integrate several factors to determine the effective forage value. The derived models are planned to be used in remote sensing analyses, whereby the launch of new satellites (e.g. ESA´s Sentinel-2) and the availability of routinely processed vegetation indices (e.g. Envisat MERIS terrestrial chlorophyll index MTCI; Boyd et al. (2011)) will foster an in-depth analysis of vegetation states in the research area. A successful transfer will enable a monitoring of rangeland states over wide spatial and temporal ranges, which could be of great value for the documentation of combined effects of climate change and land-use change on forage provision, and for the optimization of livestock management in these degradation-prone regions.

2.2 DRIVERS OF FORAGE SUPPLY IN SAVANNA ECOSYSTEMS

Abstract

Livestock rearing is the most important agricultural activity in global drylands, making forage supply an essential ecosystem service (ES). Most drylands will experience increasing levels of climatic aridity and land-use pressure in the future. As few studies account for combined effects of these global change drivers, we still have a limited understanding of how these drivers jointly shape forage supply. Here, the concept of social-ecological systems (SESs) is useful, as it helps to formalize the complex interrelationships of drivers. Taking advantage of steep gradients of climatic aridity and land-use pressure in West Africa, we applied a crossed space-for-time substitution to capture combined effects of climate and land-use change on forage supply. We have operationalized the SES concept via structural equation modelling, and analysed how drivers directly or indirectly affected forage quantity, quality and their integrated proxy (metabolisable energy yield). Results demonstrate that contemporary dryland SESs are mainly controlled by land-use, which has often been used as a proxy for other variables, such as climatic aridity. Aridity was also directly linked to a higher risk of vegetation degradation, indicating that future drylands will be less resilient to grazing pressures. The importance of land-use drivers for ES provision implies that sustainable grazing management could potentially mitigate detrimental climate change effects. However, model effects mediated by intermediate variables, such as aridity, short-term vegetation dynamics, and weather fluctuations, make it extremely difficult to predict climate change effects on ESs. Integrating structural equation modelling into the well-defined SES concept is thus highly useful to disentangle complex interdependencies of global change drivers in dryland rangelands, and to analyse drivers' direct and indirect effects on ESs. Our novel approach can thus foster a deeper understanding of patterns and mechanisms driving ecosystem service supply in drylands, which is essential for establishing sustainable management under conditions of global change.

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Introduction

Livestock rearing is the dominant land-use sector on earth and plays a critical role in human nutrition and food security (Godber & Wall, 2014; Herrero & Thornton, 2013). Approximately 40 percent of the world's agricultural gross domestic product is derived from livestock rearing, providing one-third of mankind's protein supply and supporting livelihoods for one billion of the world's poor in the developing world (Steinfeld et al., 2006). Livestock rearing is also the primary type of land-use in drylands, which comprise arid, semi-arid and dry-subhumid ecosystems (Adeel et al., 2005). As drylands support many socially disadvantaged groups that rely heavily on grazing and farming (Godber & Wall, 2014), livelihood security in drylands is highly dependent on the "forage" ecosystem service that is provided by rangeland vegetation (Adeel et al., 2005; Phelps & Kaplan, 2017). Livestock production often compensates for negative effects of climatic, market and disease shocks on livelihood security by diversifying risk and increasing income (Martin et al., 2016; Thornton et al., 2007).

In many dryland regions such as those in Sub-Saharan Africa, increasing local demands for livestock products will also increase demands for forage (Herrero & Thornton, 2013). These changing land-use patterns may exert detrimental feedbacks on ecosystem functions and on the supply of ecosystem services (ESs), including forage provision (Guuroh et al., 2018; Reynolds et al., 2007; Vandandorj et al., 2017). Various abiotic and biotic factors may interactively contribute to this "feedback spiral" towards degradation (King & Hobbs, 2006).

Besides changing land-use, climate change constitutes another severe threat to dryland rangelands worldwide (Maestre, Salguero-Gómez, & Quero, 2012; Ruppert et al., 2015). Climate change effects on drylands will be particularly strong, with most drylands projected to experience an even more pronounced climatic aridity (Maestre et al., 2012). Although it is widely acknowledged that global drivers of change interact, we still have a limited understanding how they shape ES supply through their various interdependencies (Oliver & Morecroft, 2014). In this regard, Guuroh et al. (2018) recently contributed to a better understanding of the relative importance of global change drivers on ES supply, including forage provision, in Sub-Saharan Africa. However, this study was not designed to investigate direct and indirect effects of land-use and climate change on ESs and this remains a critical knowledge gap.

To formalize and disentangle the joint effects of global change drivers on ES provision from dryland rangelands, the concept of social-ecological systems (SESs) is particularly useful (Huber-Sannwald et al., 2012; Linstädter et al., 2016). Within an SES, a dynamic co-adaptation exists between human decision-making and ES provision. Hence, human and ecological subsystems are coupled and interlinked by diverse drivers operating across multiple scales (Stafford Smith et al., 2007).

Another characteristic of dryland rangelands is the high intra-seasonal and short-term variability in forage provision. Firstly, forage provision in seasonal climates is always subject to periodic fluctuations due to the phenological development of plants (Butt et al., 2011). Secondly, variable weather conditions can trigger substantial short-term vegetation responses, especially at the beginning of the growing season (Brüser et al., 2014). Finally, disturbances such as grazing and fire may cause an immediate loss of plant biomass (Augustine & McNaughton, 2006; Oesterheld et al., 1999). Due to a variety of anthropogenic disturbances overlaying other sources of spatio-temporal variability, spatio-temporal patterns in forage provision are particularly complex in sub-Saharan Africa (Brottem et al., 2014).

Besides the inherent complexity of dryland SESs and the importance of intra-seasonal and short-term variation, there is a third reason for our limited understanding of how global environmental changes modulate ES provision on a regional scale: global change implies changes in multiple biotic and abiotic factors. This hampers the disentanglement of their direct and indirect effects on ecosystem services. In this context, structural equation modelling (SEM) is increasingly applied, as it allows direct and indirect drivers (i.e. the effect that a variable A exerts over a variable B by a mediator variable C), as well as combined effects on target variables to be separated (Eldridge & Delgado-Baquerizo, 2017; Gaitan et al., 2014; Ochoa-Hueso et al., 2018). These effects are usually shown via path diagrams with linkages or pathways between variables.

Identifying such effect pathways and the variables that mediate these effects (via indirect linkages) would support monitoring and early-warning systems to foster adaptive livestock management strategies (Stuth et al., 2005). Furthermore, knowing direct and indirect effects of climate and land-use change on forage supply at a regional level would enhance our ability to understand and predict impacts of global change on this critical ecosystem service (Martin et al., 2014).

To achieve such an understanding, one of the most efficient study approaches is to exploit natural gradients in climate and land-use (Oliver & Morecroft, 2014). Here we take advantage of the fact that in West Africa’s Sudanian savannas, a steep regional gradient of climatic aridity is overlain by sharp local gradients of land-use pressure (Ferner et al., 2015; Guuroh et al., 2018; Ouédraogo et al., 2015). Hence, we can use a crossed space-for-time substitution for both climate and land-use change, while previous ES studies typically focussed either on climate change (Valencia, Quero, & Maestre, 2016; Yuan et al., 2017) or land-use change (Allan et al., 2015) and assessed only a limited set of drivers (Oliver & Morecroft, 2014).

The aim of our study is to assess the simultaneous effects of climate change and land use on the quality and quantity of the African drylands' forage supply. Uniquely, our study *formalizes* the direct and indirect effects of global drivers of change through a SES approach, and *quantifies* direct and indirect effects via structural equation modelling (SEM). We test three hypotheses: (H1) Combining the SES framework with SEM helps to disentangle causal relationships underlying land-use and climate change effects on forage supply; (H2) SEM also helps to detect feedback pathways of long-term and short-term drivers; and (H3) global environmental change has strong indirect effects on forage supply that can either strengthen or counteract its direct effects.

Materials and Methods

Study area

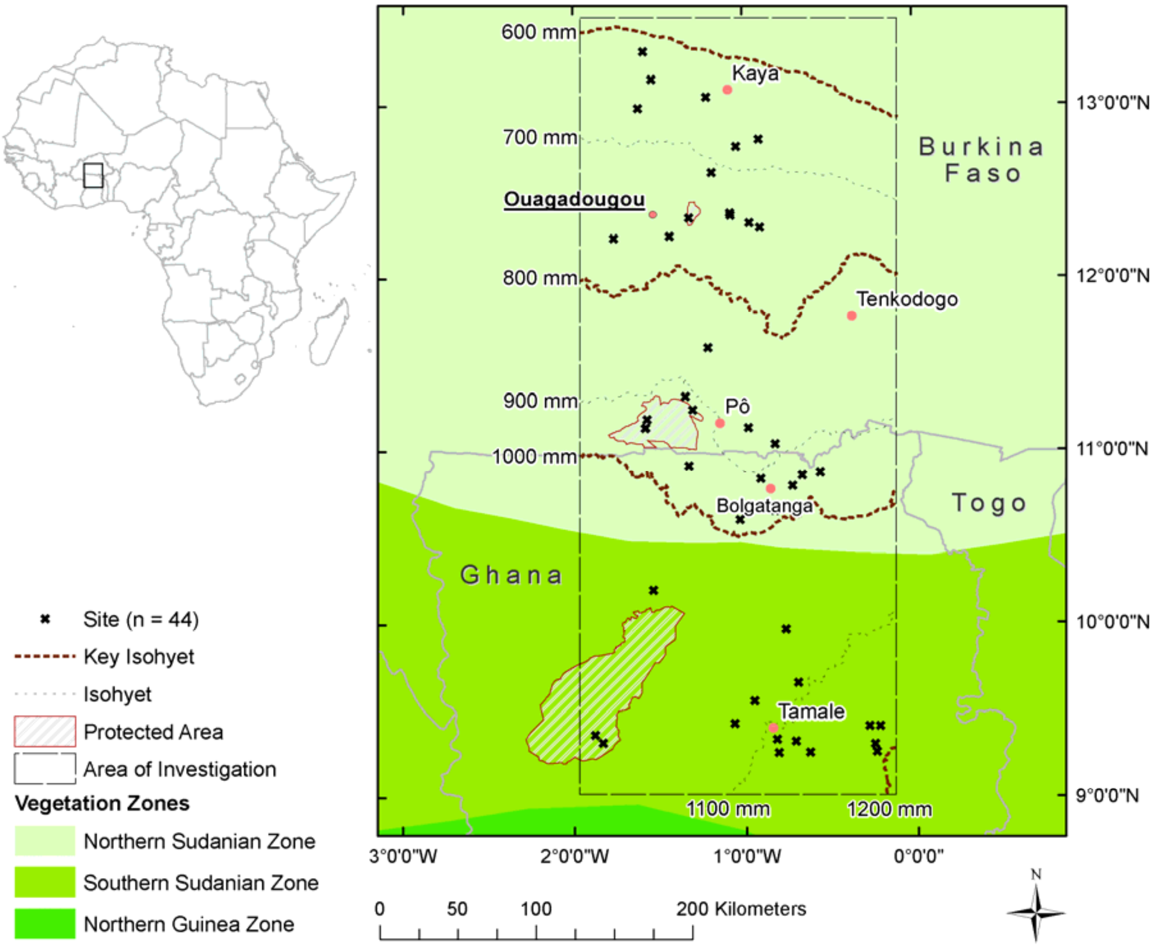

Figure 2.2-1: Map of study area and sites with vegetation zones based on White (1983). The study area was separated into three zones of increasing aridity based on isohyets: 1200-1000 mm = zone 1, 1000-800 mm = zone 2, 800-600 mm = zone 3 (www.worldclim.org). In each zone, the full length of the respective land-use pressure gradient was sampled, ranging from ungrazed sites in protected areas over moderately grazed sites to heavily grazed sites close to settlements.

The study area spans northern Ghana to central Burkina Faso, and covers ca. 106 000 km² in West Africa's Sudanian savannas (**Figure 2.2-1**). The climate is characterized by a rainy season from May to August in the north, and April to October in the southeast. The area includes a steep gradient of climatic aridity, ranging from a mean annual precipitation (MAP) of 600 mm in the north to 1200 mm in the southeast (**Figure 2.2-1**). This corresponds to aridity indices (Middleton & Thomas, 1997) of 0.31 (semi-arid) to 0.69 (humid).

The main geological units are migmatite in the north and sandstone in the south (Ferner et al., 2015), corresponding to plinthosols and lixisols as the main soil types (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012). The Sudanian savannas in the study area (**Figure 2.2-1**) constitute a belt of farmed parkland savanna (Maranz, 2009) with >3000 years of livestock farming (Ballouche & Neumann, 1995). Outside protected areas, recent land-use consists of a mosaic of fallows, non-arable land, forest fragments and fields (Friedl et al., 2010).

Study design

Social-ecological systems

We used a social-ecological system (SES) perspective (Huber-Sannwald et al., 2012; Linstädter et al., 2016) to asses the dynamic coadaptation between human decision-making and the environment's provision of ecosystem services. Hence, we distinguished between a SES's human and ecological subsystem; these are coupled and interlinked by diverse drivers operating across multiple scales (Stafford Smith et al., 2007). According to the SES framework proposed by Stafford Smith et al. (2007), three types of drivers are distinguishable, resulting in six possible interdependencies (**Figure 2.2-2a**). These are ecological drivers (E) which interact within the ecological subsystem (E→E); external drivers and shocks (X) that directly affect the ecological (X→E) or social subsystem (X→S); and land-use drivers (S) which interact within the social subsystem (S→S) or constitute a linkage between the social and the ecological subsystem (S→E). Together these drivers determine vital ESs including forage provision (Bennett, Peterson, & Gordon, 2009; Duru et al., 2015) and thus a key ecological-to-social linkage (E→S). Besides filling the "black box" of interactions within the ecological subsystem (E→E), our study mainly addresses the question of how global change drivers – with climate change as an external driver (X) and land-use change as a social driver (S) – shape ecosystem characteristics and ES supply through their various interactions (**Figure 2.2-2b**).

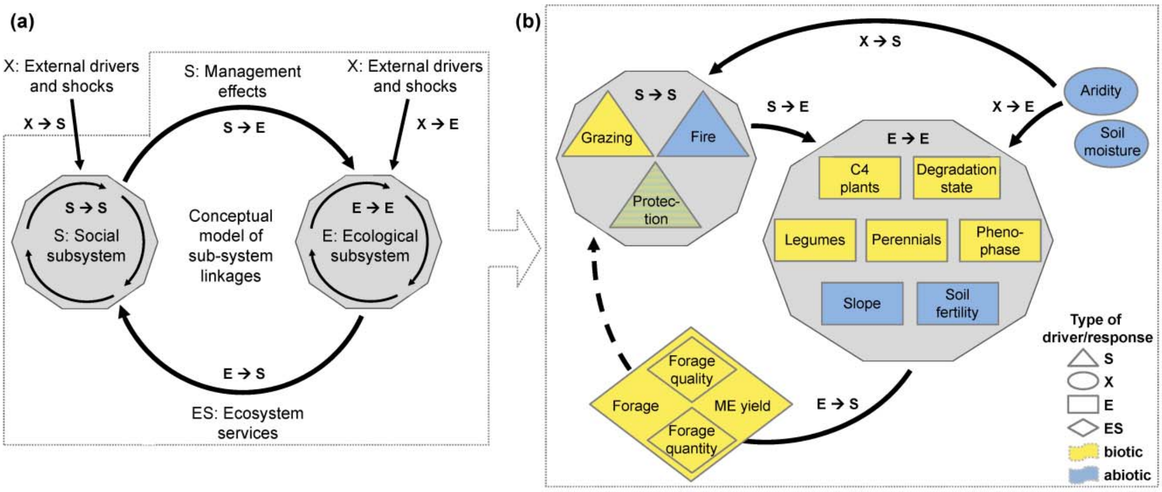

Figure 2.2-2: Conceptual framework for studying interactive effects of climate change and land-use change on ecosystem services. (a) Six types of interdependencies are distinguishable within a complex social-ecological system (SES); modified from Stafford Smith et al. (2007): Interactions within the social subsystem (S→S) and the ecological subsystem (E→E) are accompanied by linkages between subsystems, i.e. land-use effects (S→E) and ecosystem services (E→S). Furthermore, external drivers and shocks may affect the social (X→S) and the ecological subsystem (X→E). (b) This study explores how these interdependencies modulate the ecosystem service of forage provision (E→S) in dryland rangelands under conditions of global change. It considers climate change effects on both subsystems (X→E, X→S) and land-use change effects on the ecological subsystem (S→E). The driver "protection" combines biotic as well as abiotic effects.

Sampling design

Our sampling design intended to capture land-use and topo-edaphic gradients along the regional climatic gradient. For this purpose, we stratified our sampling into three zones of climatic aridity (Figure 2.2-1). In each zone, we covered the full length of the respective land-use gradient by including heavily grazed sites as well as non-grazed sites in protected areas. We further stratified sampling at our study sites by topographic position (upslope, footslope and lowland) and geology to capture soil diversity. Field data were collected during the rainy seasons 2012 (June-September) and 2013 (July-October) to include inter- and intra-seasonal dynamics of forage provision. To capture the spatio-temporal variability of various biotic and abiotic drivers, we combined data publicly available at the site level with data recorded at the level of vegetation plots (**Table 2.2-1**, see also **Table A - 1** in the Appendix). Here, most variables affecting the savanna ecosystem (e.g., fire) were acquired from GIS data, while data describing interactions within the ecosystem (e.g., phenophase) were predominantly collected in the field at the (sub-)plot level.

We sampled 44 sites along the study area, 14 in the most arid zone, 15 in the intermediate zone, and 15 in the least arid zone). Each site accounted for 3-5 plots (10 m x 10 m) located at different slope positions within rangelands (i.e. fallows that had not been cultivated for >10 years, or non-arable land; Ouédraogo et al. (2015)), obtaining a total of 302 plots. Finally, three circular subplots of 1 m^2 were randomly placed in each plot. See details on the variables measured at the site, plot and subplot level below.

Data acquisition

External drivers (X)

Data on climate and weather fluctuations were obtained at the site level, assembling several datasets. From the WorldClim database (www.worldclim.org), we derived climate variables such as mean temperature, MAP, and precipitation seasonality (**Table 2.2-1**). We further calculated aridity indices (Middleton & Thomas, 1997) using the formula by Thornthwaite (1948) and extracted data on potential evapotranspiration from CGIAR-CSI Global-Aridity and Global-PET Database (Trabucco & Zomer, 2009) using the formula by Hargreaves, Hargreaves, and Riley (1985).

We captured intra-seasonal weather fluctuations as short-term changes in soil moisture. This was estimated via two variables acquired from NASA (Owe et al., 2008) based on passive microwave remote sensing. We acquired soil moisture for the fieldwork data collection day (interpolated if necessary), as well as “accumulated soil moisture” for the fieldwork data collection day and two preceding days.

Ecosystem properties (E)

Vascular plant species were recorded with their phenological stage, cover and average height at the subplot level by visual interpretation, and were subsequently averaged to plot level. We distinguished six phenological stages (germinating, sprouting, shooting, flowering, fruiting, and senescent), using a simplified BBCH scale (Hess et al., 1997). Species' biovolume data (cover x height) and phenological stage were aggregated into communities' phenological stage ("phenophase"), following procedures for community-aggregated traits (Vile, Shipley, & Garnier, 2006). We also grouped species' biovolume data into the biovolume of (i) legumes versus non-legumes, (ii) annuals versus perennials, and (iii) species with a C_4 photosynthetic pathway versus non-C_4 species.

At the plot level, topsoil samples (0-4 cm) were assembled from five randomly placed subsamples to determine carbon (C) and nitrogen (N) content. Moreover, we used negative RESTREND (Global Residual Trend of Sum Normalized Difference Vegetation Index; Wessels et al. (2007)) values as a proxy for human-induced degradation at the site level. Degradation severity was calculated as the negative residuals of a regression between annual rainfall and annual sum NDVI. If the sum NDVI was lower than expected in response to received rainfall, a reduced rain-use-efficiency and thus vegetation degradation could be assumed.

Land-use (S)

At the plot level, visible signs of herbivore activities (trampling, droppings, and the removal of standing biomass) were used for an expert estimate of recent grazing pressure (following Linstädter et al., 2014); ranging from 0 (ungrazed) to 4 (heavily grazed). We defined sites as being protected according to the classification by IUCN and UNEP-WCMC (2013). Fire frequency data were acquired from MODIS Active Fire Detections extracted from MCD14ML distributed by NASA FIRMS.

Forage provision (ES)

As forage quality (i.e. metabolisable energy content; ME; **Table 2.2-1**) is time and cost intensive to sample, we estimated the ME content of plots by applying partial least squares regression (PLSR; Wold et al. (2001)) parameterized with vegetation reflectance obtained from a full-range spectrometer (FieldSpec 3 Hi-Res Portable Spectroradiometer; ASD Inc., Boulder, CO, USA). The regression was established for the same research area and found to be robust (R^2 of 0.56 and errors of 11.7% in validation), allowing their use here as a dependent variable (see Ferner et al. (2015) for further information).

We used total aboveground biomass (tBM) as a proxy for forage quantity (Oomen et al., 2016b). Based on species' biovolume, phenology and functional group affiliation, linear models were used to estimate tBM per subplot (for details on methodology see Guuroh et al. (2018)). We also calculated the product of forage quality and quantity as an integrative proxy of forage supply from rangelands (metabolisable energy yield, MEY). All tBM, ME and MEY calculations were carried out per subplot and then averaged to plot level.

Data analysis

To disentangle joint effects of global change and land-use drivers on forage provision, we used Partial Least Squares Path Modelling (PLS-PM; Tenenhaus et al. (2005)), a non-parametric, composite-based type of structural equation modelling (SEM). SEMs are multivariate methods that allow the linkage of measurable attributes (i.e. indicator variables) to underlying hypotheses or theoretical concepts by means of (unobserved) latent variables (LV). LVs are constructs of predictors or indicators merged, in this particular case based on correlations, into a single robust variable or component (i.e. similar to the components of PCA or CCA, but in a supervised manner).

Path models can also quantify direct, indirect and combined effects on target variables (Grace et al., 2010). In PLS-PM, this is done by performing linear regressions for each interaction, obtaining model coefficients (i.e. path coefficients (β)). Indirect effects are exerted by modulating intermediate variables, and can either strengthen a driver's direct effect (unidirectional effects; i.e. with same signs of path coefficients), or weaken them (opposing effects, i.e. different signs of path coefficients). Even when SEM presented similar model accuracies to regressions and ordinations methods, the modulation of the intermediate effects demonstrated a higher potential for the identification of key functioning parameters (Grace, 2003). Up to now, PLS-PM has been used mainly in the social sciences, but also has demonstrated applicability in the geosciences (Lopatin et al., 2015). See **Table 2.2-1** for the composition of the LVs and their indicators.

Table 2.2-1: Characteristics of variables belonging to four variable sets considered in this study (land-use drivers, external drivers (climate and weather drivers), internal drivers within the ecological subsystem, and ecosystem services), and variable affiliation to a "latent variable" (LV) in structural equation models. Data source is coded as OD = own data and PA = publicly available data. Spatial scale refers to the spatial level of available data, while temporal scale refers to the time span between a change of a driver and the responses of the ecosystem service "forage". Minimum, median and maximum values are given if applicable. For further information, see **Table A - 1** (Appendix).

Variable	**Data source**	**Spatial scale**	**Temporal scale of response**	**Type of variable/ unit***	**Min**	**Median**	**Max**	**LV affiliation**
Land-use drivers (S)								
Grazing pressure	OD	Plot	Months to years	Ordinal (0-4)	0	2*	4	Grazing
Fire frequency	PA	Site	Years	Events 10 km^{-2} $Year^{-1}$	0	1.11	57.45	Fire
Protection status	PA	Site	Years	Factor (yes/no)	-	-	-	Protection
External drivers (X)								
Aridity Index	PA	Site	Decades	Relative	0.31	0.48	0.69	Aridity
Climate zone	PA	Site	Decades	Ordinal (1-3)	1	2*	3	Aridity
Mean annual precipitation	PA	Site	Decades	mm	631	932	1200	Aridity
Potential evapotranspiration	PA	Site	Decades	mm day^{-1}	1822	1918	2024	Aridity
Precipitation of driest quarter	PA	Site	Decades	mm	0	7	19	Aridity
Temperature seasonality	PA	Site	Decades	SD*100	152.2	184.5	234.0	Aridity
Accumulated soil moisture	PA	Site	Days to weeks	%	0	42	83	Soil moisture
Soil moisture	PA	Site	Days to weeks	%	0	14	28	Soil moisture

Internal drivers (ecosystem characteristics; E)								
Relative abundance of C$_4$ plants	OD	Plot	Years	%	0	0.61	0.99	C4 plants
Degradation	PA	Site	Years to decades	RS	0	0	0.0078	Degradation state
Relative abundance of legumes	OD	Plot	Years	%	0	0.061	0.83	Legumes
Relative abundance of perennials	OD	Plot	Years	%	0.002	0.45	1	Perennials
Community-aggregated phenology	OD	Plot	Weeks	Ordinal (0-5)	1.06	2.37*	4.93	Phenophase
Slope position	OD	Plot	Millennia	Ordinal (0-3)	1	2*	3	Slope
Soil C content	OD	Plot	Weeks	%	0.29	1.08	4.71	Soil fertility
Soil N content	OD	Plot	Weeks	%	0.031	0.071	0.32	Soil fertility
Ecosystem services								
Metabolisable energy	OD	Plot		MJ kg^{-1} DM	3.47	9.03	14.71	Forage quality
Total aboveground biomass	OD	Plot		g m^{-2}	22.08	121.8	655.2	Forage quantity
Metabolisable energy yield	OD	Plot		GJ ME ha^{-1}	2.27	11.03	55.22	Forage ME yield

* Ordinal data were treated as quasi-numerical. SD = Standard deviation; CV = Coefficient of variation; RS = Residuals.

Through SEM, we modelled the complex network of all important interactions between driver and response variables. This included the calibration of three separate sub-models to capture relationships between the three main driver types. To understand the direct and indirect effects of drivers on ecosystem service provision, we finally calibrated separate sub-models for our three proxies of forage provision. Since SEM results depend on the specification of underlying hypotheses (Grace et al., 2010), expert knowledge was required to build a conceptual *a priori* model. Our final path model (**Table A - 2** in the Appendix) specifies all hypothesized linkages between LVs and forage provision based on the findings of previous studies in (African) rangelands.

Concerning management effects on the ecological subsystem (S→E), it has been found that grazing (Moreno García et al., 2014), fire (Colombaroli et al., 2014; Koerner & Collins, 2014), and protection (Traoré et al., 2012) can significantly shape vegetation structure, composition and the nutritional quality of forage. On the other hand, external drivers (X→E) such as climatic aridity can also influence vegetation composition and structure (Barthelemy et al., 2015; Gaitan et al., 2014). Within the ecological subsystem (E→E), it can be anticipated that plants vary in forage quality and quantity depending on their photosynthetic pathway (Sage & Kubien, 2003), N-fixing ability (Phelan et al., 2015) and life cycle (Le Houérou, 1980; Ruppert et al., 2015).

Due to data availability and model structure, all LVs were defined as endogenous, i.e. dependent on at least one exogenous (independent) LV, except protection, aridity, soil moisture and slope, which were defined as independent exogenous variables. As data was acquired at different spatial scales, and since drivers operated on varying temporal scales (**Table 2.2-1**), we formulated an additional rule set. First, no LV measured at plot level was expected to have an influence on LVs from site level, except for grazing pressure, which was considered to represent an attribute true for a larger area. Second, soil moisture, as an external LV highly variable in space and time, was expected to only influence the response variables, which we assumed would respond within days to weeks (**Table 2.2-1**). Lastly, LVs that usually remain stable over several years (protection, fire frequency, aridity, degradation, and slope) were not expected to alter plant phenology during the study years.

For PLS-PM model validation, bootstrapping was performed with 1500 repetitions. All statistical analyses were undertaken in R (R Development Core Team, 2011). Path model fitting and analysis was primarily carried out through the “plspm” package (Sanchez, 2013).

Results

Causal relationships shaping the social-ecological systems

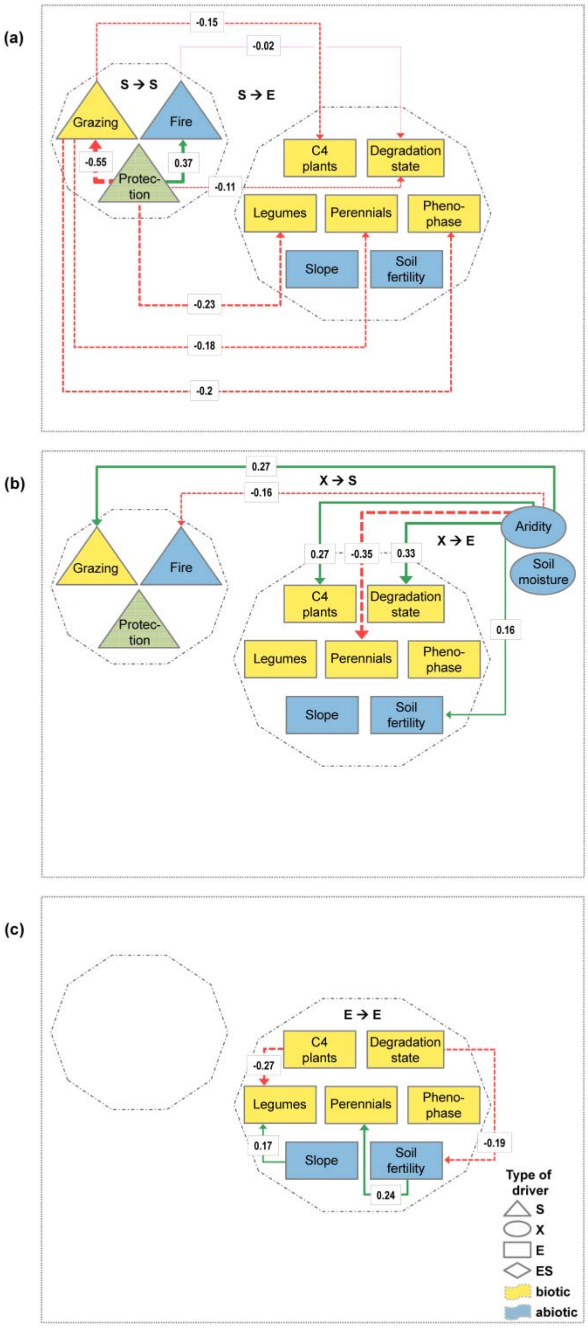

Figure 2.2-3: Conceptual framework for studying interactive effects of climate change and land-use change on ecosystem services. (a) Six types of interdependencies are distinguishable within a complex social-ecological system (SES); modified from Stafford Smith et al. (2007): Interactions within the social subsystem (S→S) and the ecological subsystem (E→E) are accompanied by linkages between subsystems, i.e. land-use effects (S→E) and ecosystem services (E→S). Furthermore, external drivers and shocks may affect the social (X→S) and the ecological subsystem (X→E). (b) This study explores how these interdependencies modulate the ecosystem service of forage provision (E→S) in dryland rangelands under conditions of global change. It considers climate change effects on both subsystems (X→E, X→S) and land-use change effects on the ecological subsystem (S→E). The driver "protection" combines biotic as well as abiotic effects.

We found complex relationships shaping the studied SESs (**Figure 2.2-3**). Considering land-use drivers (**Figure 2.2-3a**), the strongest effects were found between drivers themselves (S→S), i.e. between protection and grazing pressure (-0.55) and protection and fire frequency (0.37). The various land-use effects on ecosystem characteristics (S→E) were all negative in nature, with particularly strong effects of grazing on phenophase (-0.20), but with almost no fire effects.

The external climatic driver “aridity” had by far the most important and most diverse effects in studied SESs (**Figure 2.2-3b**), while “soil moisture” demonstrated only non-significant effects. Aridity did not only influence the ecological subsystem directly but also indirectly via several feedback pathways. Specifically, it modulated two management interventions (X→S): Increasing aridity increased grazing pressure (0.27) but decreased fire frequency (-0.16). Hence, strong and direct interactions between climate and land-use drivers were found. Direct aridity effects on ecosystems (X→E) included a negative effect (-0.35) on the abundance of perennial plants and a positive effect (0.27) on C_4 plants. Aridity also increased the likelihood of vegetation degradation (0.33).

Several interdependencies were discernible within the ecological subsystem (**Figure 2.2-3c**; E→E). Abiotic factors only affected biotic factors (e.g., soil fertility increased perennial plant abundance). In contrast, biotic factors could either interact between themselves – with high C_4 plant abundance decreasing legume abundance (-0.27) – or by feedback on abiotic factors. Importantly, vegetation degradation had negative effects on soil fertility.

Important drivers of the ecosystem service of forage supply

Separate models for forage quality, quantity and their combination (MEY) explained 45%, 70% and 52% of variation, respectively (**Figure 2.2-4**). With respect to global change drivers, we found that climatic aridity had no direct impact on any aspect of forage supply. However, it did have a negative impact on forage quality, although slightly under the threshold for significance. Among land-use drivers, grazing pressure had strong, contrary effects on forage quality and quantity (ME: 0.23, tBM: -0.27). Unsurprisingly, protection had opposite effects, but was only significant for tBM (0.4) and MEY (0.33). Fire frequency had no significant effects on forage provision.

Besides global change drivers, seasonal vegetation dynamics (phenophase), weather fluctuations (soil moisture) and degradation state were also significant drivers of forage supply, while other ecosystem characteristics such as slope position and abundance of perennials were of minor importance. Like grazing, phenophase also had contrary effects on forage quantity and quality (ME: -0.24, tBM: 0.31).

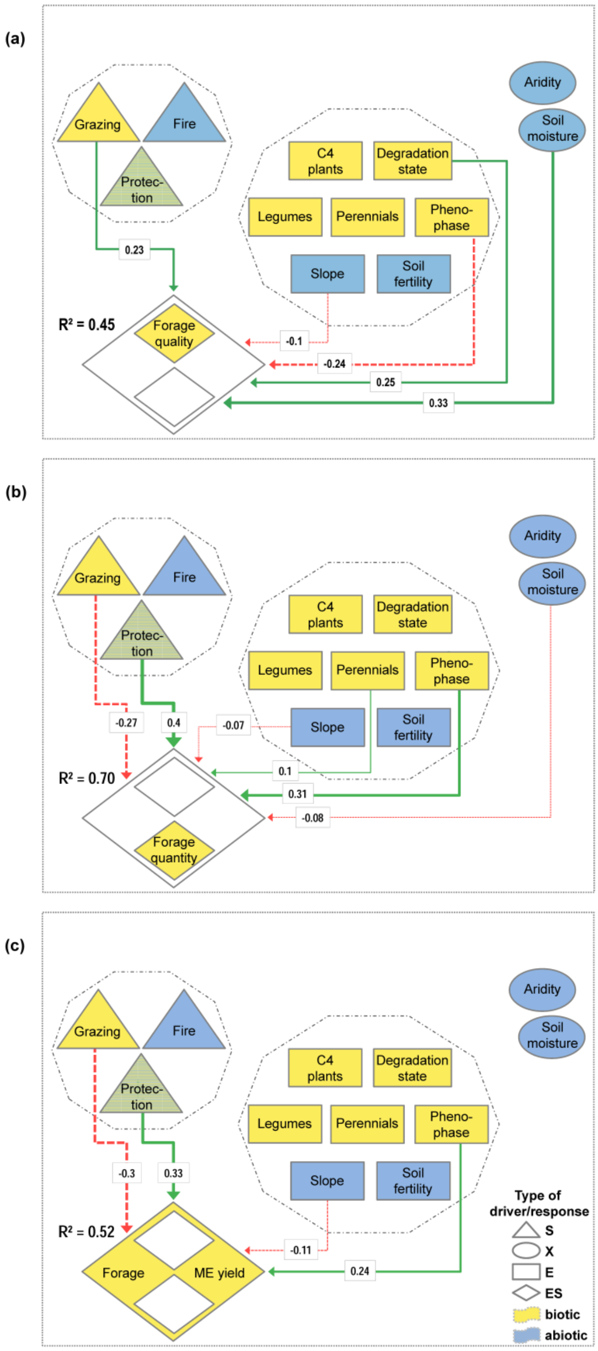

Figure 2.2-4: Final SEMs for (a) forage quality (ME), (b) forage quantity (tBM) and (c) forage ME yield (MEY). Path coefficients on the arrows, as well as arrow size, show the strength of effects. Green-solid arrows indicate positive causal relations, while red-dashed arrows depict negative relations.

Direct and indirect controls of forage supply

Indirect effects of global change drivers on forage supply were often strong; in the case of protection and climatic aridity, they were even stronger than their direct effects. With respect to effect direction, considerably more unidirectional effects (indirect effects strengthening direct effects) were observable than opposing effects (indirect effects weakening direct effects; see **Figure 2.2-5**). Protection was the most important indirect driver, reducing forage quality via its effects on two other land-use drivers, but increasing forage quantity and MEY. Interestingly, the most notable opposing effect occurred regarding climatic aridity. Stronger indirect effects always reversed its small, non-significant, direct effects on forage supply (negative on ME, positive on tBM and MEY).

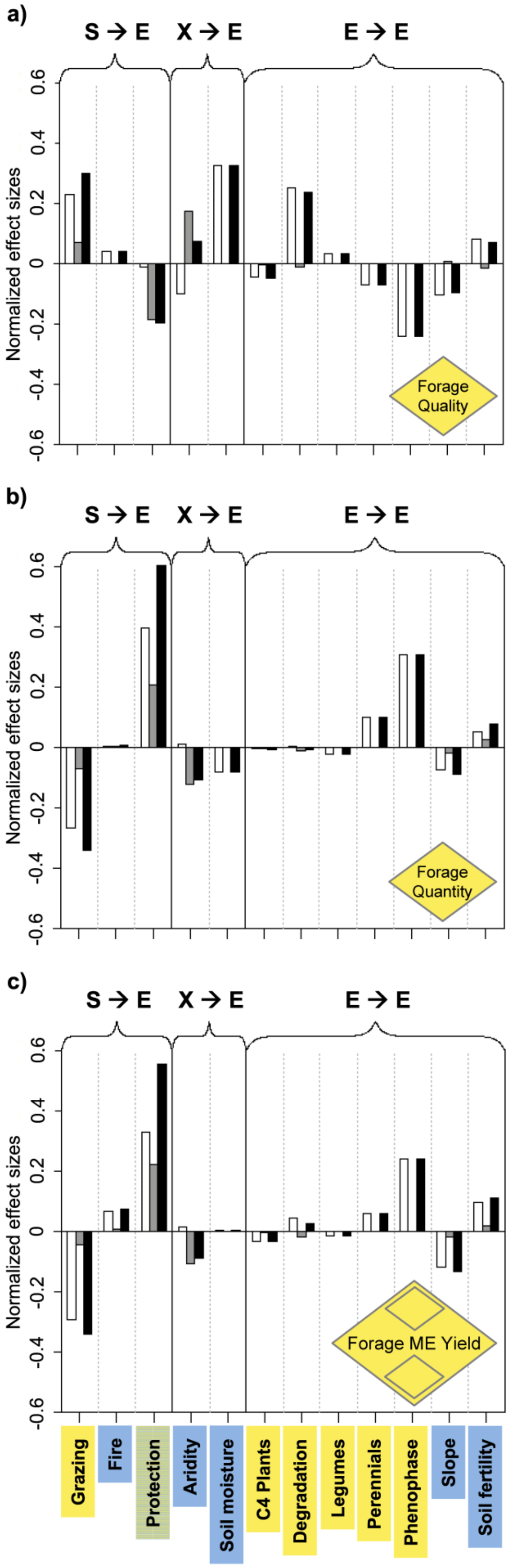

Figure 2.2-5: Normalized direct (white), indirect (grey) and total effects (black) of driver variables in SEMs on (a) forage quality, (b) forage quantity and (c) forage ME yield.

Discussion

Disentangling causal relationships in the study SESs

We found complex relationships within the studied SESs. First, we found strong interdependencies within the social subsystem (S→S). The negative effect of protection on grazing pressure seems trivial, as livestock grazing is prohibited within protected areas. However, we observed that this law is increasingly violated (also confirmed by previous studies; Ouédraogo et al. (2015); Traoré et al. (2012)). Positive protection effects on fire incidence can be explained by a higher fire frequency within protected parks (Gregoire & Simonetti, 2010) due to regular management fires (Ouédraogo et al., 2015).

Second, we detected multiple effects of land-use drivers on ecosystem characteristics (S→E). The strong negative effect of grazing on phenophase can be explained by rejuvenation after disturbance (Breedt, Dreber, & Kellner, 2013). In contrast, fire effects on ecosystem characteristics were non-significant, probably due to the fact that fire tends to have positive effects on ecosystem functions in more humid areas and negative effects under more arid conditions (Oesterheld et al., 1999).

Third, climatic aridity primarily shaped the ecological subsystem as an external filter (X→E). It had negative effects on perennial plants and C_3 plants, which is in line with previous observations that aridity favours annuals (Linstädter et al., 2014) and heat-adapted C_4 plants (Sage & Kubien, 2003). Climatic aridity was also directly linked to the incidence of vegetation degradation, underlining the vulnerability of more arid regions to degradation (Adeel et al., 2005). Note that the RESTREND method statistically removes effects of precipitation changes on rain-use-efficiency, allowing a focus on human-induced degradation (see Fensholt et al., 2013; Wessels et al., 2007). Moreover, climatic aridity was found to be an important mediator of land-use drivers (X→S), most notably grazing pressure. This underlines that these key drivers of global change are not independent (Munson et al., 2016; Oliver & Morecroft, 2014; Turner, 1998a).

For example, livestock keeping is more common under arid conditions, where grazing allows the utilization of land not suitable for cropping (Fetzel et al., 2017).

Finally, in the ecological subsystem (E→E), the negative effect of C_4 plants on legumes was particularly strong. This is not surprising, as perennial C_4 grasses dominate the grass layer of protected areas (Bocksberger et al., 2016; Zimmermann et al., 2015). In contrast, legumes may only gain dominance under conditions of overgrazing, when they are no longer outcompeted by perennial grasses (Linstädter et al., 2014).

Effects of drivers with short-term and long-term variation

We used a crossed space-for-time substitution to capture interactive effects of climate and land-use change on forage attributes. As these drivers can affect forage provision at different spatial and temporal scales (Linstädter et al., 2016), we aimed to capture both short- and long-term variation. We could thus compare the effects of global change drivers acting over comparatively large temporal scales to short-term effects of weather fluctuations and vegetation dynamics. Among drivers of the first type, grazing and protection were particularly important. Grazing increased forage quality by stimulating the regrowth of high-quality plant biomass (Changwony et al., 2015; Moreno García et al., 2014). Additionally, grazing can trigger a shift towards plant communities dominated by palatable and nutritious forage plants, creating “grazing lawns” (Hempson et al., 2015). Lawn grasses feature high leaf-to-stem ratios, foliar N levels (Moreno García et al., 2014) and thus a high digestibility (Chaves et al., 2006).

Grazing and protection were also important drivers of forage quantity and MEY. While Flombaum, Yahdjian, and Sala (2017) corroborate this result, Guuroh et al. (2018) found the season's accumulated precipitation to be the most important driver of tBM. We found that grazing negatively affects forage quantity, which is in line with a meta-analysis of dryland rangelands' biomass production (Ruppert et al., 2012b). As we did not control for grazing offtake, this partly reflects the direct loss of biomass through grazing (Oesterheld et al., 1999). Moreover, factors such as intra-seasonal biomass turnover and compensatory growth were not accounted for (Fetzel et al., 2017). Therefore, standing biomass is only a rough proxy of biomass production (Oomen et al., 2016b).

The strong influence of degradation on forage quality could be explained by the method we used for degradation assessment: based on a regression between annual rainfall and NDVI (Wessels et al., 2007). A low NDVI response to received rainfall implies a reduced rain-use-efficiency and thus human-induced degradation, most likely caused by high grazing pressure (Rasmussen et al., 2014) which increases forage quality.

Among drivers with short-term variation, plant phenology and soil moisture were particularly important for forage supply. Phenology strongly reduced forage quality (e.g. Guuroh et al., 2018), being the most important factor modulating forage quality of tropical pastures due to a progressive decline in digestibility and crude protein (Atta-Krah & Reynolds, 1989; Changwony et al., 2015). Hence, management strategies like grazing or mowing that counteract phenological progress often improve forage quality (Hughes et al., 2013b). Phenology was found to have strong effects on forage quantity, reflecting biomass accumulation in the growth period.

We observed only a small, negative relationship between soil moisture and biomass, contrary to the known influence of stochastic seasonal fluctuations in rainfall and soil moisture on primary production in dryland grasslands (Lauenroth & Sala, 1992). We assume that reduced soil moisture at the end of the rainy season (i.e. at the time of maximum biomass accumulation) is responsible for this effect.

Strength and direction of global change drivers' indirect effects

As expected from previous studies applying structural equation modelling to quantify global change drivers on ES supply (Allan et al., 2015; Gaitan et al., 2014), we found important indirect effects in the model. Notably, a higher aridity indirectly reduced biomass production and metabolisable energy yield via altered land-use practices. Thus, understanding climate change effects on forage supply requires consideration of complex feedback pathways in dryland SESs (Linstädter et al., 2016), especially (but not solely) via aridification effects on land-use.

Conclusion

Altogether, our results suggest that our novel SES framework, operationalized via structural equation modelling, greatly helps in disentangling complex effects of global change on ecosystem service supply. The approach helps to find effects of key mediator variables on the whole system which would otherwise not be easily measured. With respect to climate change mitigation, a sustainable grazing management could potentially mitigate the detrimental effects of increased climatic aridity (see Guuroh et al. (2018)). Nevertheless, the presence of indirect feedback pathways, short-term weather fluctuations, and vegetation dynamics make it difficult to upscale and predict global change effects on ESs. Hence, early-warning systems need to capture interdependent effects of changing climate and land-use on ES supply at an appropriate spatial and temporal resolution.

2.3 MODEL APPLICATION FOR FORAGE MONITORING

Abstract

Forage supply of tropical savannas plays a crucial role in rural Africa. Consequently, installing a monitoring system that can deliver reliable spatio-temporal information about the quantity and quality of forage from these ecosystems could help in better managing as well as understanding the dynamics of this valuable resource. Field spectroscopy has proved to be a suitable tool to estimate forage supply in African savannas, however, our study investigates whether models for green biomass (gBM), metabolisable energy (ME), acid detergent fibre (ADF), amylase-treated neutral detergent fibre (aNDF), ash (XA), and phosphorus (P) can be calibrated using the spectral resolution of satellite sensors and which actual sensor (hyperspectral or multispectral) provides the best data for forage monitoring purposes. Finally, we aimed at using the resulting forage maps to identify important drivers of forage supply. Our results indicate that the hyperspectral resolution of Hyperion contains more relevant information and thus allowed for calibrating models with a better fit. When applied to actual satellite data, the greater quality of the multispectral Sentinel-2 satellite data resulted in more realistic forage maps. We conclude that until now, none of the investigated satellites provide optimal qualities for regular monitoring purposes. Nonetheless, making use of a time series over three years of Hyperion data, our analysis corroborates phenology and water availability (cumulated precipitation) as the most important drivers of forage supply at this broad spatial scale. Future hyperspectral satellite missions like EnMAP, combining the high level of information from Hyperion with the good data quality and temporal resolution of Sentinel-2, will provide the prerequisites to install a regular monitoring service.

This chapter is a paper draft in preparation for submission:

Ferner, J., Linstädter, A., Rogaß, C., Südekum, K.-H., Schmidtlein, S., 2018. Towards a monitoring of forage resources in tropical savannas: Going multispectral or hyperspectral?

Introduction

In Africa, low-input livestock production systems are common and depend strongly on savanna rangelands (Egeru et al., 2015). Forage services (i.e. quantity and quality) of savanna ecosystems are the main drivers of farmers' management decisions (Duru et al., 2015). Moreover, the foraging behaviour, habitat selection and migration of wild herbivores are related to forage availability (Van der Graaf et al., 2007). Given the importance of forage services from savanna rangelands, there is a need to establish sustainable land-use and management practices, particularly in the context of ongoing global environmental change (Gaitan et al., 2014).

Due to the high variability of forage services, sustainable management strategies require techniques that can help to effectively map and continuously monitor the spatial extent, amount, and temporal development of forage services (Prince, Becker-Reshef, & Rishmawi, 2009; van Lynden & Mantel, 2001). Thus, regional forage biomass and nutrient maps provided by a regular monitoring system would present highly useful information to managers of protected areas and farmers (Ramoelo et al., 2012). Conventional methods for the determination of forage services require direct measurements, which are time-consuming, expensive and based on extensive fieldwork. Furthermore, these estimates are restricted to the selected sites, whereas reliable estimates are needed at broader extents and in a spatially contiguous manner (Psomas et al., 2011). Therefore remote sensing can play a pivotal role for the estimation of forage quantity and quality and its temporal variations (Phillips et al., 2009).

Very early attempts to monitor intra- and interannual variation in vegetation biomass using satellite imagery were undertaken in the Sahel (Prince, 1991; Tucker et al., 1983; Tucker et al., 1985), often based on the Normalized Difference Vegetation Index (NDVI) (Diallo et al., 1991). However, a growing number of recent studies of vegetation biomass estimation are based on (airborne) hyperspectral data and concurrent field sampling, e.g. for the investigation of biomass production in mixed grassland ecosystems (Beeri et al., 2007; Cho et al., 2007; Kooistra et al., 2006; Mirik et al., 2005; Suzuki et al., 2012). Furthermore, statistical relationships between vegetation biomass and spectral data have been established using field spectrometer measurements resampled to match band definition of hyperspectral or multispectral satellite sensors (Hansen & Schjoerring, 2003; Psomas et al., 2011; Xavier et al., 2006), but only a few studies have actually tested the application of such field-developed statistical models to satellite imagery (Anderson et al., 2004; Zha et al., 2003).

One of the most important potential applications of hyperspectral remote sensing in vegetation studies is the mapping of forage quality (Townsend et al., 2003). The vegetation´s reflectance can be measured on the ground using field spectroscopy and related to forage quality characteristics, e.g. foliar nitrogen (N), phosphorus (P) (Sanches et al., 2013), acid detergent fibre (ADF), neutral detergent fibre (NDF), ash (XA), and metabolisable energy (ME) (Pullanagari et al., 2012).

Furthermore, several studies (e.g. Beeri et al. (2007); Ferwerda (2005)) have shown that airborne and spaceborne data can also be used as a proxy for the forage quality of vegetation canopies. For example, Mutanga and Skidmore (2004a), Skidmore et al. (2010) and Mutanga and Kumar (2007) successfully mapped N, P and polyphenols, respectively, of African savannas based on HyMap data while Knox et al. (2011) used the CAO Alpha sensor to map N, P and fibre. Other studies have concentrated on mapping the N status of tree species making use of Hyperion imagery (Coops et al., 2003; Martin et al., 2008; Smith et al., 2003; Townsend et al., 2003).

Using multispectral WorldView-2 data, Zengeya et al. (2012) have mapped N concentration of vegetation in Zimbabwe, while Ramoelo et al. (2012) used RapidEye imagery to estimate and map foliar and canopy N in South Africa. The vegetation N content is suited to mapping as it has a high correlation with chlorophylls (Netto et al., 2005).

Upscaling from point-based observations to reveal their spatial pattern is one possible way to create maps of forage resources. Here, field spectroscopy is a starting point for upscaling data from the leaf to the canopy and finally the pixel level (Milton et al., 2009). However, these attempts are hampered by the fact that plant-light interactions that allow one to infer the vegetation´s quantity and quality are scale dependent (Ollinger, 2010), e.g. the amount and distribution of senescent and green leaf material as well as soil cover plays a crucial role at coarser spatial resolutions (Asner, 1998). Thus, it still remains a challenge to transfer the techniques developed in the field to spaceborne imagery.

To assess the best data basis to eventually set up a regular forage monitoring programme, we tested data from two different satellite sensor types providing data with different spatial and spectral properties. While hyperspectral sensors like Hyperion with its many narrow bands appear to be better suited for the upscaling of hyperspectral models from field spectroscopy (Durante et al., 2014), a multispectral system such as Sentinel-2 should also be tested as it has been shown to be comparable and even more reliable than hyperspectral sensors (Transon et al., 2018) with a higher spatial and temporal resolution. The latter is particularly important for savannas, where the vegetation has a rapid phenological cycle due to a short rainy season and the time of image acquisition is limited (Vintrou et al., 2014). As both Hyperion and Sentinel-2 have their advantages, they are compared in this mapping exercise to identify the best suited sensor for a forage monitoring.

Biomass and forage quality of rangelands are highly variable in both space and time (Durante et al., 2014). Thus, understanding how biotic and abiotic factors control forage production can support sustainable land-use practices. Potential drivers causing variation in space are related to abiotic factors like soil characteristics, landform characteristics and water availability, as well as grazing pressure depending on e.g. available forage species and distance to water. Variation in time might be caused by the vegetation´s phenological development, varying weather conditions and management decisions (Durante et al., 2014).

In African rangelands, rainfall is regarded as the most important driver of forage biomass production (e.g. (Anyamba et al., 2014); Anyamba and Tucker (2005); Egeru et al. (2015); (Hickler et al., 2005; Huber, Fensholt, & Rasmussen, 2011)) while forage quality is expected to depend primarily on the vegetation’s phenological development (Penning de Vries & Djitèye, 1982) and plant species composition (Knox et al., 2012). In addition, West Africa is characterized by a latitudinal gradient of rainfall leading to north-south changes in vegetative productivity and nutritive quality (Le Houérou, 1980; Penning de Vries & Djitèye, 1982) accompanying variation of phenology (Butt et al., 2011). These particular environmental features will support our aim to investigate the most important drivers of forage supply in an African savanna at a broad spatial scale.

Due to the economic importance and high temporal and spatial variability of forage resources in rural Africa, our main objective was to develop a method, based on field spectroscopy, for estimating and mapping important forage supply variables in savanna habitats. Therefore, we aimed at evaluating the potential to upscale models, calibrated from plot-based measurements, to larger landscapes using hyperspectral and multispectral satellite data. The method should be independent of vegetation type and phenological state. A further aim was to investigate the effect of the sensor’s spectral characteristics on the transfer to satellite data. Finally, a third aim was to use the estimated maps of forage supply to explore temporal dynamics of forage in a tropical savanna. The specific questions are as follows:

1) Can we model important forage characteristics from in-situ hyperspectral data resampled to match the spectral resolution of multi- and hyperspectral satellites?

2) How does the type of sensor (hyperspectral vs. multispectral) affect the spatial transfer to satellite data?

3) Are there any patterns in the resulting maps that can aid an understanding of the reasons for dynamics in forage resources?

Material and Methods

Study area

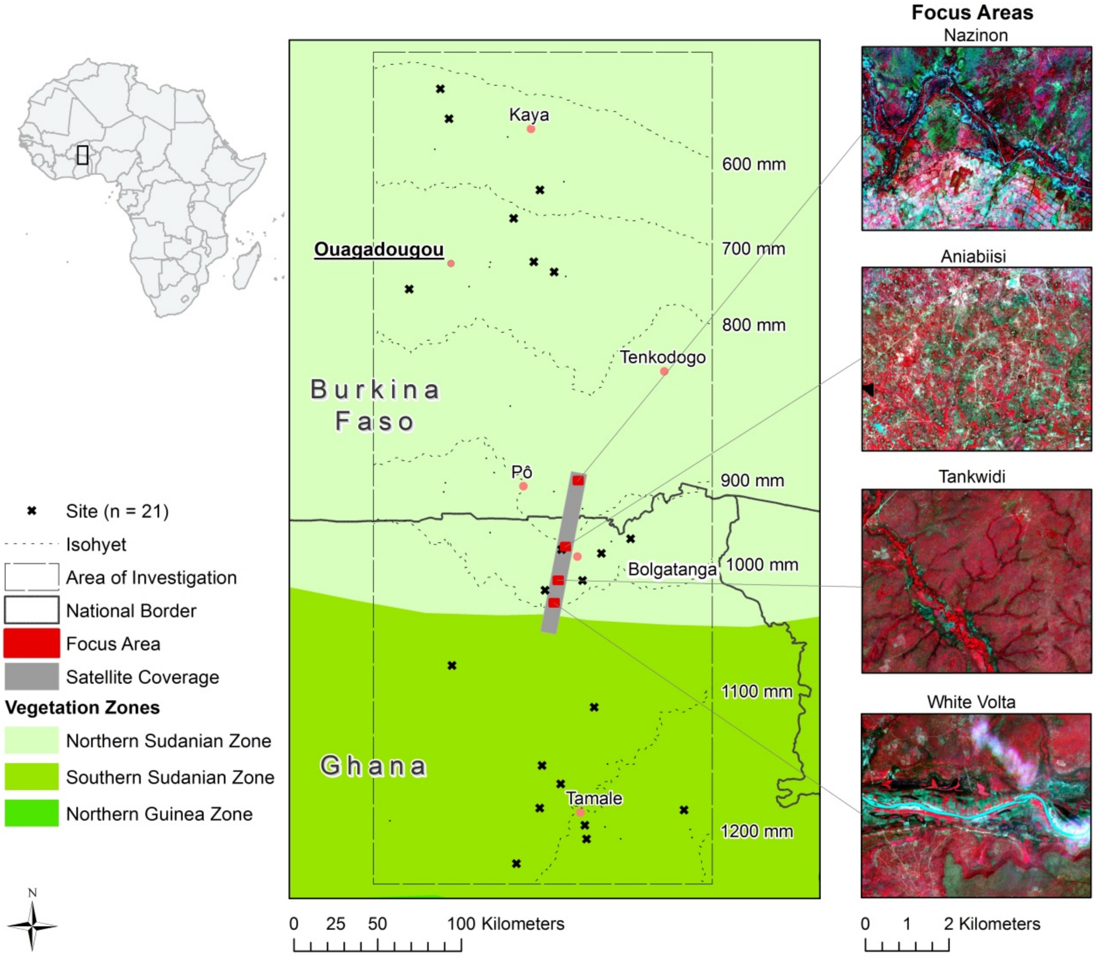

Figure 2.3-1: Map of sites for model calibration and location of mapping areas covered by satellite imagery. The broad study area covers two vegetation zones following White (1983) and is characterized by a steep increase of climatic aridity to the north (as indicated by isohyets) as well as various land-use intensities. Satellite images of focus areas at the right side show Sentinel-2 imagery acquired on 19.10.2016.

This study combines investigations from two different spatial scales. First, spectrometric models of forage supply were calibrated using data collected from sites along a climatic gradient representative of West Africa´s Sudanian savannas (Ferner et al., 2015). Second, spectrometric models were resampled and applied on satellite imagery covering four focus areas located in the centre of the climate gradient.

The broad area of investigation (i.e. climate gradient) of ca. 100 000 km² reaches from northern Ghana to central Burkina Faso covering the Northern and Southern Sudanian zone of West Africa´s Sudanian savanna (**Figure 2.3-1**). The climate is tropical, with a rainy season from May to August in the north, and April to October in the southeast. Main geological units are migmatite in the north and sandstone in the south (Ferner et al., 2015).

Four focus areas are located along the climate gradient in the border region of Ghana and Burkina Faso (**Figure 2.3-1**). The most northern area, Nazinon, covers part of the Nazinon river basin in Burkina Faso. The three focus areas in Ghana are Aniabiisi, located north-west of Bolgatanga which is the capital of Upper East Region, Tankwidi, covering parts of the Tankwidi river basin and the surrounding forest reserve and White Volta, covering parts of the White Volta river basin. The vegetation in all areas belongs to the northern Sudanian savanna (White, 1983) and constitutes a belt of farmed parkland savanna (Maranz, 2009). Site conditions vary moderately between areas (**Table 2.3-1**). However, focus areas were chosen to depict variation due to a local climate gradient as well as a strong difference in land use, i.e. the Aniabiisi area is intensively farmed and grazed by livestock whereas the river basins constitute rather natural habitats.

Table 2.3-1: Site conditions of the four focus areas in the border region of Ghana and Burkina Faso.

		Climate[1]				Soil texture[4]		
Focus area	Country	Mean temperature [°C]	Mean annual precipitation [mm]	Main land cover[2]	Soil types[3]	Sand content [%]	Silt content [%]	Clay content [%]
Nazinon	Burkina Faso	28.1	857.4	Open deciduous woodland, closed to open shrubland, agriculture	Cambisol	56.8	25.9	17.2
Aniabiisi	Ghana	28.3	923.8	agriculture	Lixisol	53.4	29.6	17.0
Tankwidi	Ghana	28.4	981.3	Closed to open shrubland, grassland	Lixisol	61.8	22.2	15.9
White Volta	Ghana	28.3	1000.4	Closed to open shrubland	Lixisol	60.9	23.4	15.7

[1] www.worldclim.org (Hijmans et al., 2005)

[2] Gessner et al. (2015)

[3] Harmonized world soil database (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012)

[4] World soil Information (ISRIC, 2013)

Field data collection

For model calibration we collected data during the rainy season in 2012 at 21 sites spread along the north-south gradient (**Figure 2.3-1**). Spectral reflectance measurements of vegetation plots were performed using a FieldSpec 3 Hi-Res Portable Spectroradiometer (hereafter FieldSpec) (ASD Inc., Boulder, CO, USA) which detects light in a spectral range from 350 – 2500 nm (ASD Inc., 2006). For more details regarding sampling design, see Ferner et al. (2015).

After measurements, vegetation was clipped to stubble height, air-dried and shipped to the laboratory of the Institute of Animal Science, University of Bonn (Germany), where six forage variables (green biomass (gBM), metabolisable energy (ME), acid detergent fibre (ADF), amylase-treated neutral detergent fibre (aNDF), ash (XA), phosphorus (P)) were determined. Samples were oven-dried (60°C, >48 h) to obtain dry mass, which equals gBM since only predominantly vital vegetation was sampled. ME was determined based on *in vitro* gas production using the Hohenheim gas test (Menke & Steingass, 1988) as well as the sample´s crude protein content (for further details see Ferner et al. (2015)).

ADF and aNDF were determined using an ANKOM^{2000} Fiber Analyzer (ANKOM Technology Corporation, Fairport, NY). XA equals the residuals of the samples after incineration at a temperature of 550°C (method 8.1; VDLUFA (2012)) while P was determined using a spectrophotometer (method 10.6.1; VDLUFA (2012)).

Processing chain of satellite data

We aimed at an evaluation of upscaling possibilities of models derived from hyperspectral near surface remote sensing to i) hyperspectral EO-1 Hyperion satellite imagery and ii) multispectral Sentinel-2 satellite imagery. Hyperion was mounted on the Earth-Observing 1 (EO-1) spacecraft (Pearlman et al., 2003) at 705 km above sea level. It provided 220 channels covering the visible and near-infrared portions of the solar spectrum from 350 to 2600 nm in 10 nm spectral resolution and 30 m spatial resolution. Hyperion was a pushbroom instrument that could image a 7.5 km by 100 km land area per image (Datt et al., 2003).

On the other hand, Sentinel-2 is a constellation of two polar orbiting satellites equipped with an optical imaging sensor MSI (multi-spectral instrument; Brandt et al. (2015)). Here we used data from Sentinel-2A, which was launched on June 23, 2015. The satellite has 13 bands with a spatial resolution of 10 m (band 2-4, 8), 20 m (band 5-7, 8A, 11, 12), and 60 m (band 1, 9, 10) that span from the visible (VIS) and the near infrared (NIR) to the short wave infrared (SWIR; Ky-Dembele et al. (2016)). Both satellites feature different sensor characteristics (**Table 2.3-2**).

Table 2.3-2: Summary of sensor characteristics of EO-1 Hyperion and Sentinel-2.

Characteristic	EO-1 Hyperion	Sentinel-2
Launch date	21.11.2000	23.06.2015
Sensor resolution	Hyperspectral	multispectral
Number of bands (bands used for this study)	242 (152)	13 (12)
Spatial resolution	30 m	10 m (bands 2:4,8) 20 m (bands 5:7,8A,11,12) 60 m (bands 1,9,10)
Quality	low signal-to-noise ratio	high signal-to-noise ratio
Availability	freely available; mainly on order (cloud-dependant image acquisition)	freely available; in combination with Sentinel-2B a revisit time of 5 days at the equator is achieved

Preprocessing of EO-1 Hyperion images

We acquired a time series of Hyperion images (26 in total) covering at least the focus area of Aniabiisi from 2013 to 2016 (**Figure 2.3-2A**). All images were downloaded from USGS EarthExplorer (earthexplorer.usgs.gov) at a processing level of L1Gst (geometric systematic terrain corrected) or L1T (systematic terrain corrected).

Hyperion data were delivered in a raw processing state and required several preprocessing steps to generate a product that could be used for monitoring purposes. Preprocessing followed the procedure recommended by Rogass et al. (2014) and included a de-striping technique, half image SWIR shift as well as interpolation of dead pixels using smoothing and dead column substitution. Subsequently, bands from the VNIR and SWIR sensors were co-registered and a local log-polar phase correlation and best fit polynomial modelling applied. In a final step, images were spectrally smoothed using a Gaussian filter with sigma=2. Afterwards, all images were atmospherically corrected using ENVI FLAASH and lastly all bands affected by considerable noise (mostly due to atmospheric water vapour) were removed to leave 152 bands for further analysis.

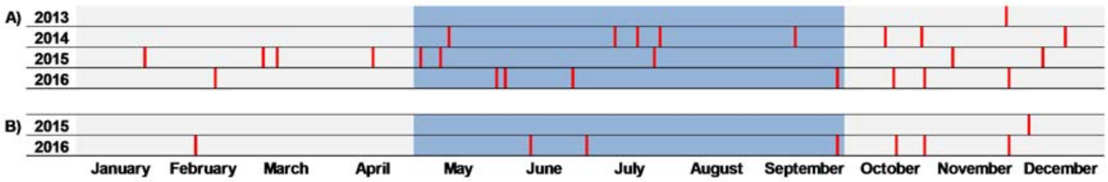

Figure 2.3-2: Temporal coverage of A) Hyperion and B) Sentinel-2 time series available for Aniabiisi area in Upper East Region, Ghana, from 2013 to 2016. Dark areas indicate time of rainy season; bright areas indicate time of dry season.

Preprocessing of Sentinel-2 images

Sentinel-2 images were acquired for eight dates (December 2015 – December 2016, **Figure 2.3-2B**) to match, as far as possible, Hyperion image availability. Imagery was atmospherically corrected using the plugin “sen2cor” within the SNAP toolbox, provided by the European Space Agency (ESA). To match Hyperion spatial coverage, two separate Sentinel-2 tiles had to be mosaicked and clipped.

Spectral unmixing procedure

To assure that forage supply models were only applied to vegetated areas, a vegetation mask was build. For this, we used MESMA (multiple endmember spectral mixture analysis; Dennison and Roberts (2003); Franke et al. (2009)) to determine the fractional cover of green vegetation on a pixel basis. We used a variety of pure field spectra of the three main land cover types in our study area, i.e. photosynthetic active vegetation (PAV), non-photosynthetic active vegetation (NPAV) and open soil (SOIL), measured with the ASD Portable Spectroradiometer. Spectra were resampled in R (R Core Team, 2014) using the sensor´s spectral response functions to match spectral resolution of satellite images, i.e. 152 bands for Hyperion and 12 bands for Sentinel-2. These spectra were used to create separate spectral libraries that served as input for MESMA calculation in Viper Tools, a plugin to ENVI developed by (Roberts, Halligan, & Dennison, 2007). MESMA output was one image with fractional coverages of PAV, NPAV and SOIL as well as MESMA residuals.

Spectral model calibration to estimate forage supply

To evaluate the effects of different spectral resolutions on model performances, full-range field spectra had to be resampled in R using the sensor´s spectral response functions to match image spectral resolution. Subsequently, we used the R package “autopls” (Schmidtlein et al., 2012) to apply partial least-squares regression with automated backward selection (PLSR; Wold et al. (2001)) to model the relations between resampled spectral data and all six forage variables.

The pre-processed images were masked to leave only pixels with a vegetation cover greater than 30% (according to MESMA results). From the masked image, MESMA residuals were subtracted, which were expected to equate to random noise, to receive natural spectral curves for each pixel. Finally, forage supply models were applied to obtain maps of estimated forage variables.

Linear model selection based on AIC

To test the influence of several potential drivers on a predicted time series of forage supply, we used linear models with a forward and backward model selection based on Akaike information criterion (AIC).

To test for the influence of phenology, a time series of MCD43A4 data was retrieved from the Moderate Resolution Imaging Spectroradiometer (MODIS) and NDVI values were calculated by (NIR - Red) / (NIR + Red) from November 2013 to December 2016. We decided to use MODIS data due to its very high temporal resolution of one to two days which helped to get a high number of usable images even during the rainy season. Data was further processed using R package “phenex” to model daily NDVI values and extract important phenological parameters; i.e. date of green-up (the point where the function of modelled NDVI values first exceeds the threshold of 0.55), date of maximum NDVI, and date of senescence (the point where the function of modelled NDVI values first falls below the threshold of 0.55). We used phenology as a factor with 1=dates before green-up, 2=dates between green-up and maximum NDVI, 3=dates between maximum NDVI and senescence and 4=dates after senescence.

Precipitation was the monthly sum of rainfall (Schneider et al., 2011) for each focus area using GPCC precipitation data provided by NOAA/OAR/ESRL PSD (via *www.esrl.noaa.gov/psd/*). Additionally, we included cumulative precipitation (cumPrecipitation) which equals the sum of precipitation of a given month plus the sum of the two preceding months.

We also tested the main land use (1: open deciduous woodland, 2: closed to open shrubland, 3: agriculture) and soil types (1: cambisol, 2: lixisol; cf. **Table 2.3-1**).

Results

Performances of PLSR models using full-range spectroradiometer data as well as spectral data resampled to hyperspectral and multispectral satellite resolution differed considerably (**Table 2.3-3**).

Table 2.3-3: Summary of model fittings for all forage characteristics using partial least-squares regression. High ${}_{adj}R^2$ values and low nRMSE values indicate a good fit of the regression models. Model validation was done via repeated (leave-one-out) cross validation (VAL_{CV}).

Forage characteristics	FieldSpec		Hyperion		Sentinel-2	
	${}_{adj}R^2$ VAL_{CV}	nRMSE [%] VAL_{CV}	${}_{adj}R^2$ VAL_{CV}	nRMSE [%] VAL_{CV}	${}_{adj}R^2$ VAL_{CV}	nRMSE [%] VAL_{CV}
Green biomass (gBM)	0.66	10.86	0.4	12.28	0.44	11.82
Metabolisable energy (ME)	0.54	11.64	0.56	11.65	0.43	13.31
Amylase-treated neutral detergent fibre (aNDF)	0.45	12.68	0.52	12.25	0.34	14.37
Acid detergent fibre (ADF)	0.34	18.67	0.42	17.85	0.03	23.13
Phosphorus (P)	0.16	19.06	0.12	19.58	0.06	20.26
Ash (XA)	0.29	14.69	0.11	13.26	-0.93	14.7

Model fits revealed that not all forage characteristics could be successfully modelled. For Hyperion, models predicting P and XA achieved low model fits, while spectral data resampled to Sentinel-2 resolution did not contain enough information to successfully model ADF, P and XA. To evaluate model plausibility and consistency between models, those bands selected for the models using the spectral resolution of the spectroradiometer, Hyperion and Sentinel-2 were compared (**Table 2.3-3**).

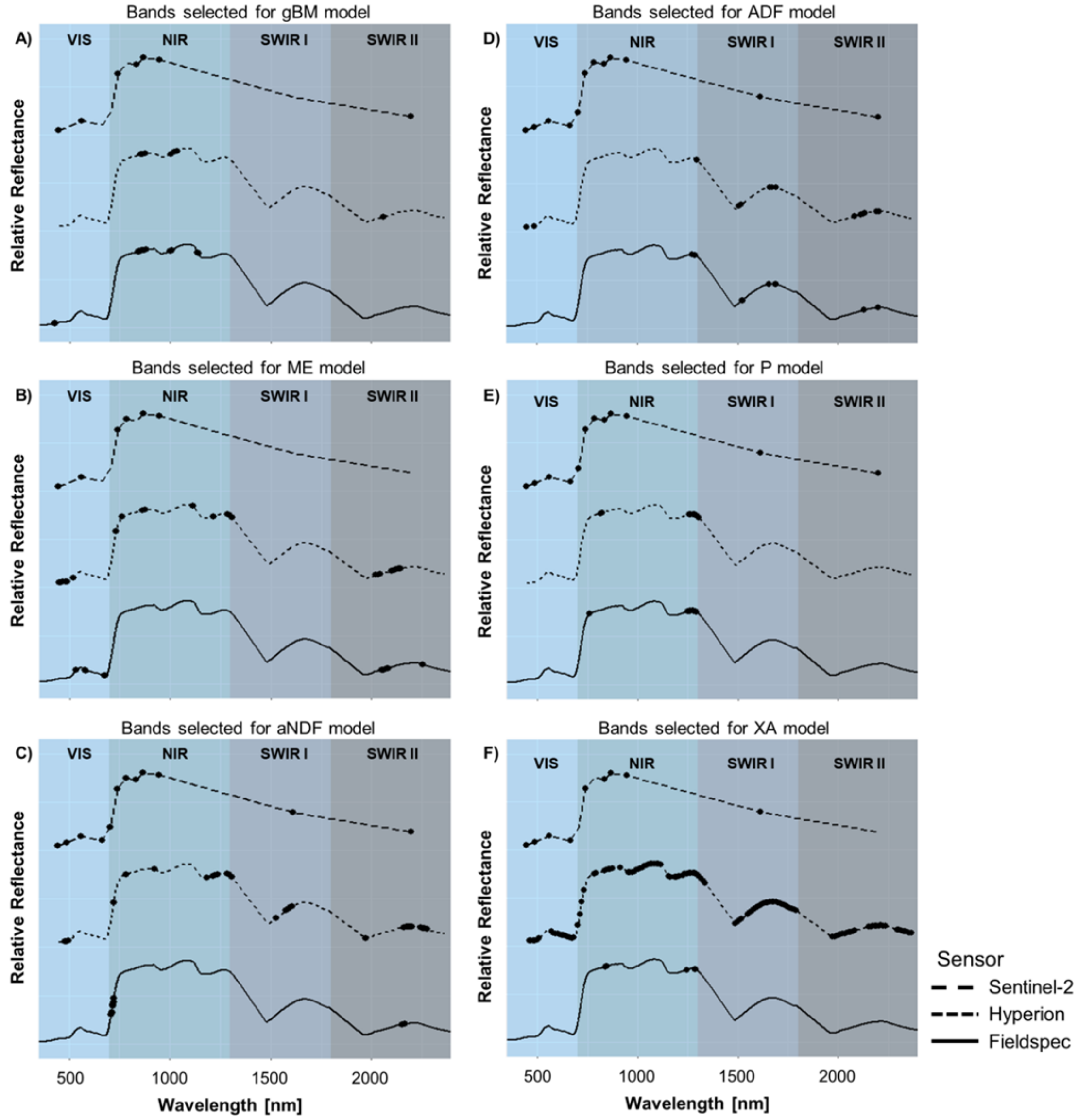

Figure 2.3-3: Spectral bands (central wavelengths) selected for the models for A) gBM, B) ME, C) aNDF, D) ADF, E) P, and F) XA using the original spectral resolution of a field spectroradiometer as well as data resampled to match the spectral resolution of Hyperion and Sentinel-2. Bands were selected from different spectral regions, i.e. visible region (VIS; 350-700 nm), near-infrared (NIR; 701-1300 nm), shortwave infrared I (SWIR I; 1301-1800 nm) and shortwave infrared II (SWIR II; 1801-2500 nm). Note that Sentinel-2 did not provide continuous spectral cover.

Many consistencies can be found between bands selected by different sensors. For gBM, the automatic band selection algorithm in autopls selected bands located in the NIR region while for ME, all models selected bands from the VIS region. For models predicting aNDF, selected bands were mainly located in the NIR (red edge) and SWIR II region. For ADF and P, many comparable bands from the SWIR and the NIR regions, respectively, were selected in the FieldSpec and the Hyperion model, while all available bands were selected in the Sentinel-2 model.

The FieldSpec model predicting XA is quite similar to the model predicting P, while the Hyperion and Sentinel-2 models included numerous bands from almost all spectral regions.

Since only model fits for gBM, ME and aNDF achieved satisfactory results for all sensors, we further concentrated on these forage characteristics. When applying the respective models to satellite imagery to generate forage supply maps, divergent results were achieved. Here, only maps for one time step (18./19.10.2016) were shown. These images provide data from the rainy season with a dense vegetation cover but only minimal cloud interference. For gBM (**Figure 2.3-4**), the pattern predicted by both satellite sensors only match for area B. Additionally, for regions C and D it can be observed that MESMA results differed, leading to many areas in the Hyperion image that were masked out before model application (which applies also for ME and aNDF models). A visual comparison with the original images (**Figure 2.3-1**) indicated that these masked areas were apparently covered by vegetation, i.e. Sentinel-2 appears to produce better results. We assume that this is caused by considerable noise in the Hyperion image. For ME and aNDF, the agreement between both satellites is even lower, with Sentinel-2 estimating generally higher ME values (**Figure 2.3-5**) but lower aNDF values than Hyperion (**Figure 2.3-6**).

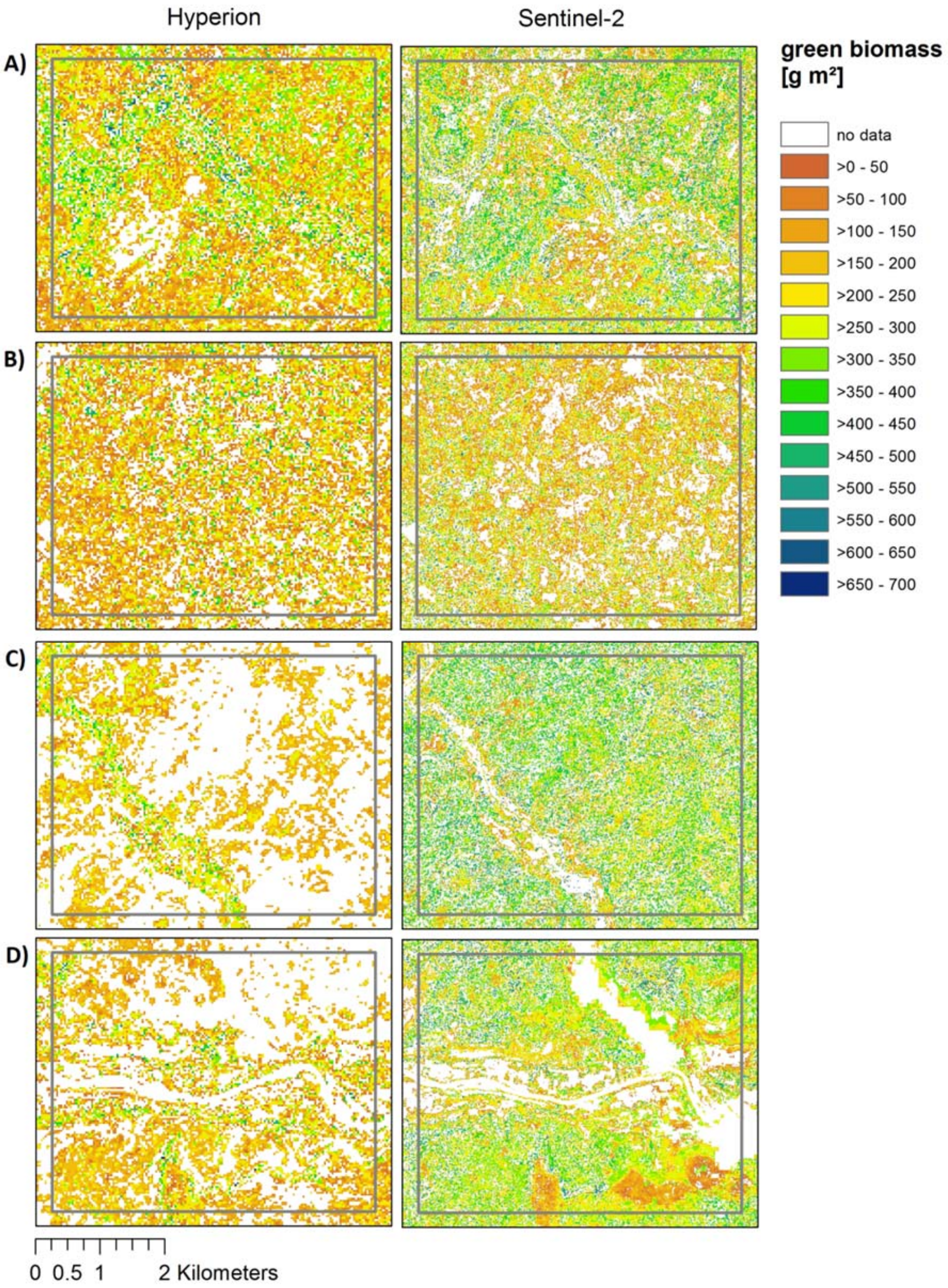

Figure 2.3-4: Forage supply map of green biomass (gBM) generated by applying models to Hyperion (18.10.16, left) and Sentinel-2 (19.10.16, right) imagery for the focus areas, i.e A) Nazinon, B) Aniabiisi, C) Tankwidi, D) White Volta.

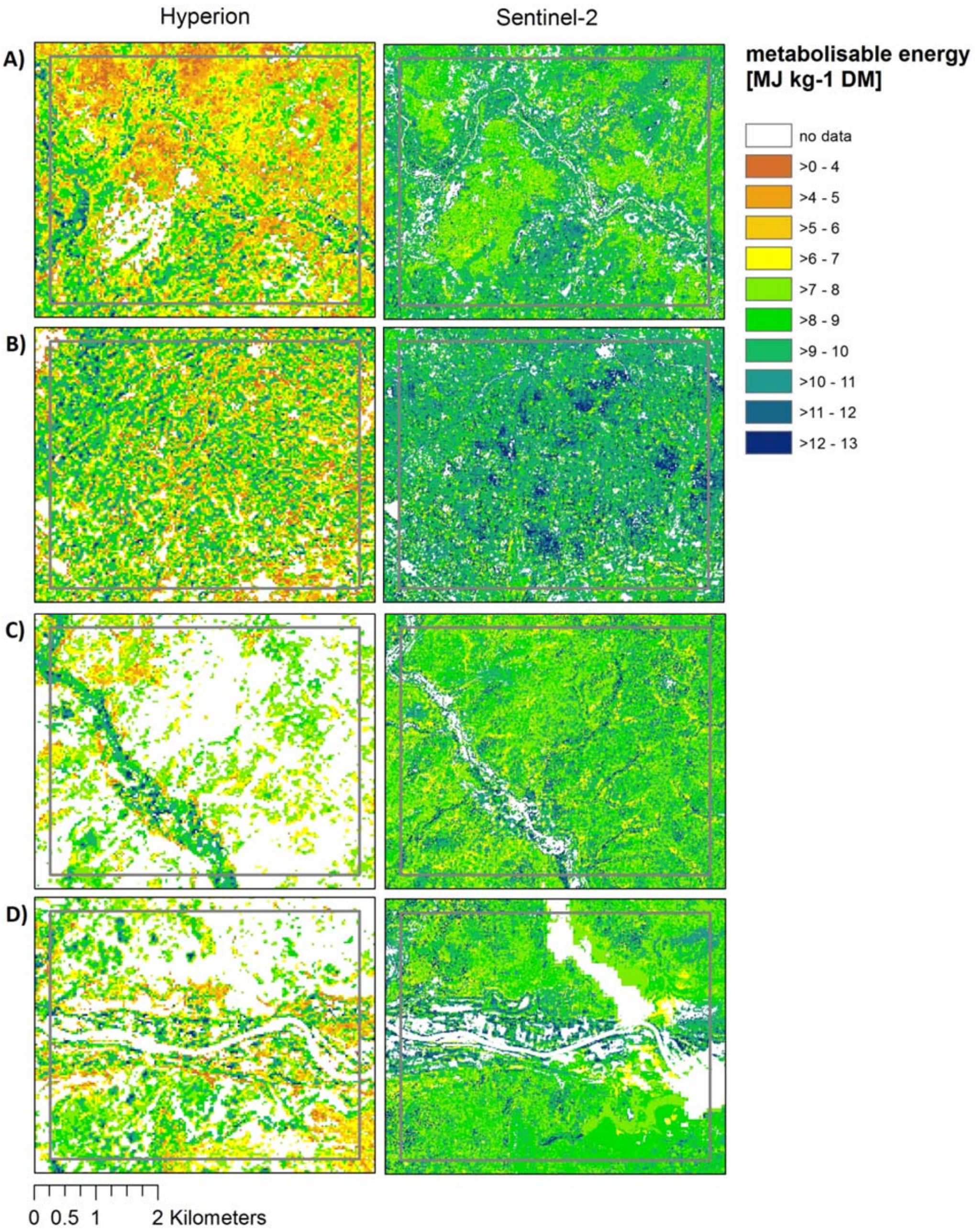

Figure 2.3-5: Forage supply map of metabolisable energy (ME) generated by applying models to Hyperion (18.10.16, left) and Sentinel-2 (19.10.16, right) imagery for the focus areas, i.e. A) Nazinon, B) Aniabiisi, C) Tankwidi, D) White Volta.

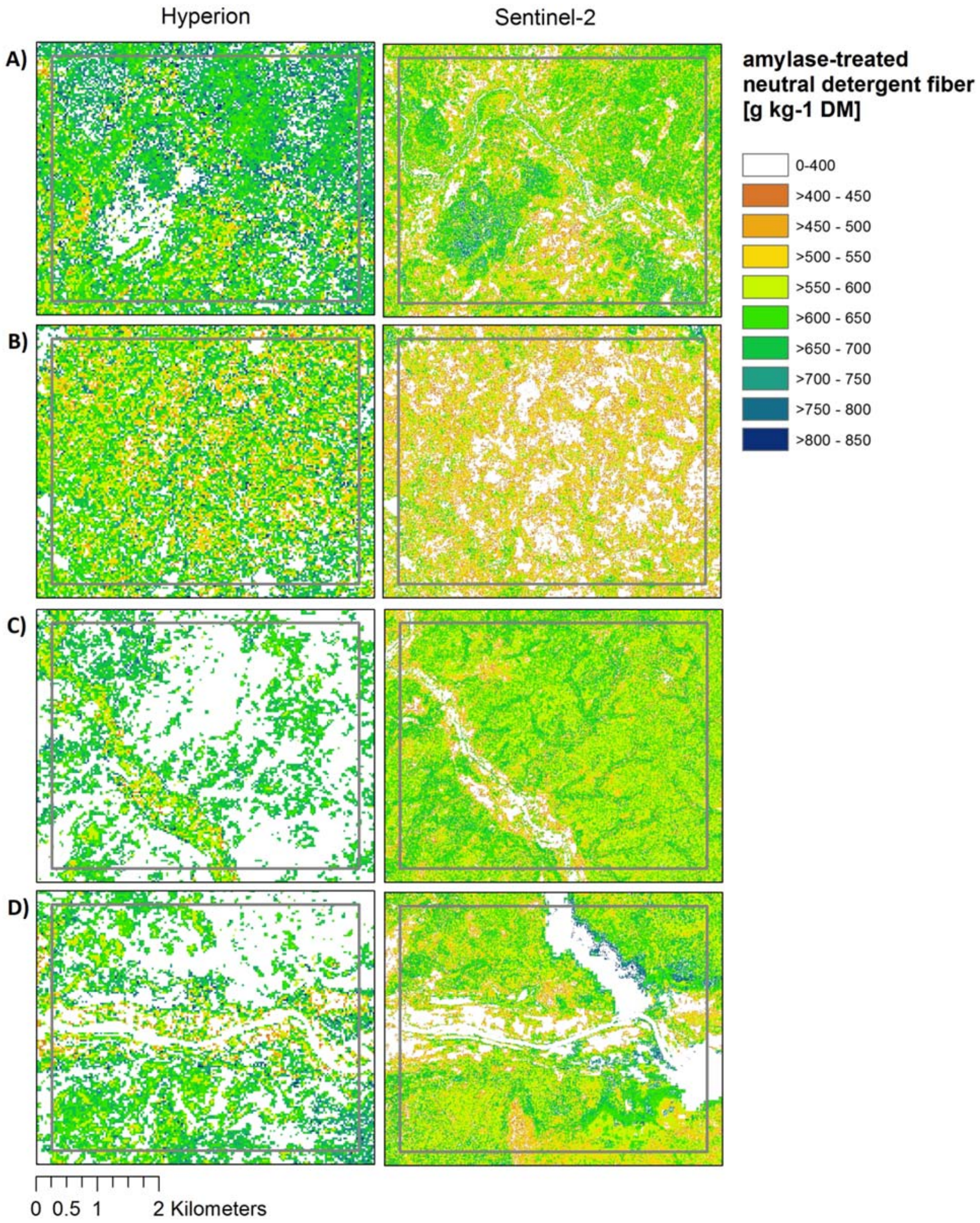

Figure 2.3-6: Forage supply map of amylase-treated neutral detergent fibre (aNDF) generated by applying models to Hyperion (18.10.16, left) and Sentinel-2 (19.10.16, right) imagery for the focus areas, i.e. A) Nazinon, B) Aniabiisi, C) Tankwidi, D) White Volta.

To better assess model plausibility, time series of forage characteristic ranges (both from Hyperion and Sentinel-2 models) were compared to values measured in the same vegetation zone, i.e. Sudanian savanna, from vegetation samples taken during the rainy season in summer 2012 (**Figure 2.3-7 - Figure 2.3-9**).

It can be seen that for all three forage characteristics, both Hyperion and Sentinel-2 models estimated values that reflect the range of values that was measured in the lab. However, only ME values showed the expected hump-shaped development over the rainy season (June 2016 – September 2016).

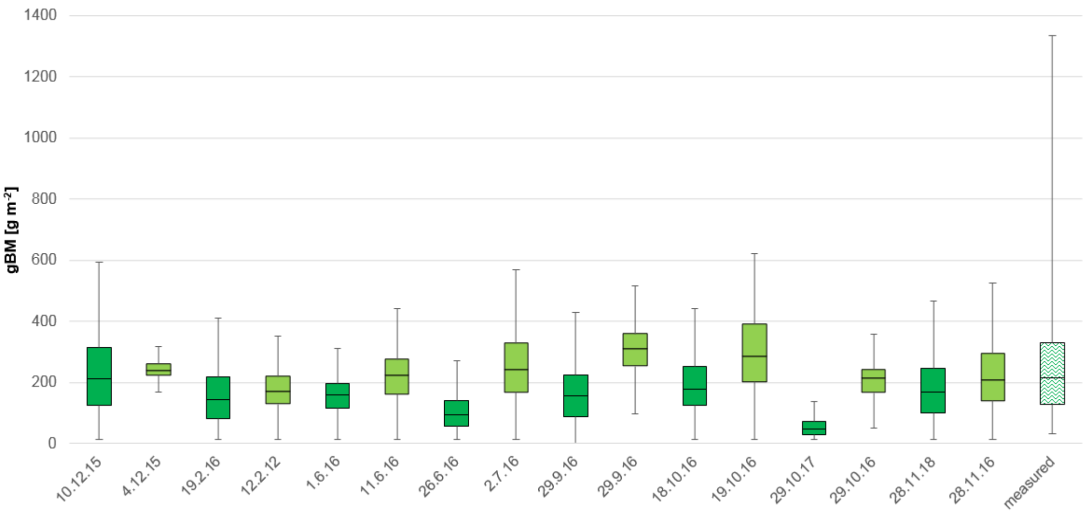

Figure 2.3-7: Time series of gBM values from all four focus areas predicted from Hyperion (dark) and Sentinel-2 (bright) images in comparison to field samples measured during summer 2012.

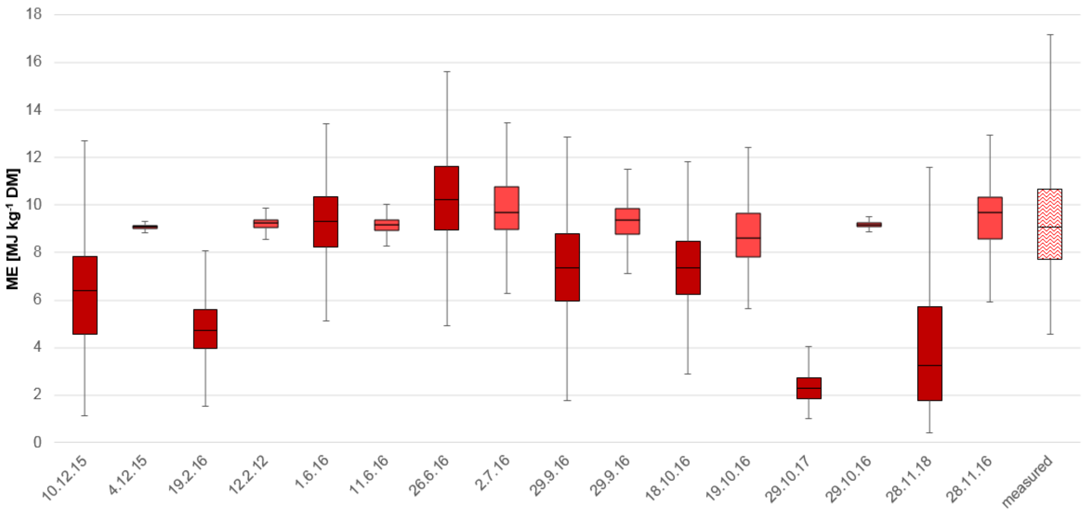

Figure 2.3-8: Time series of ME values from all four focus areas predicted from Hyperion (dark) and Sentinel-2 (bright) images in comparison to field samples measured during summer 2012.

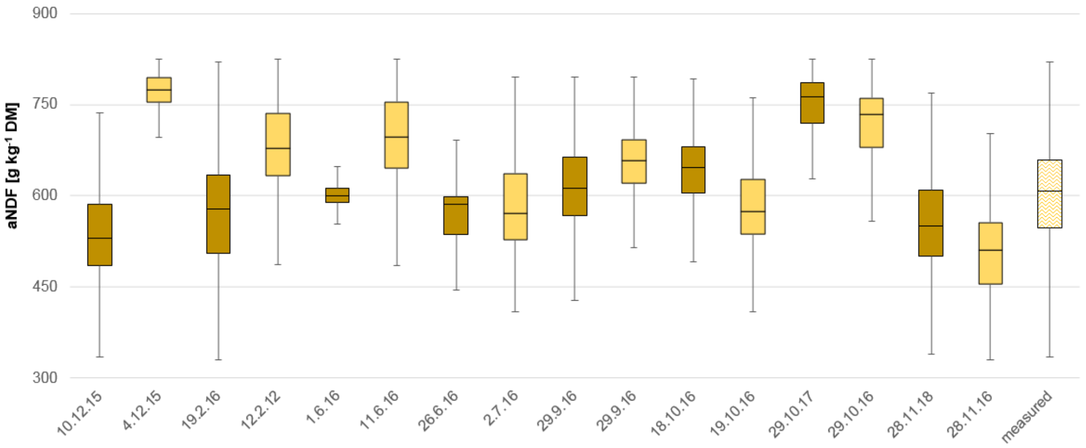

Figure 2.3-9: Time series of aNDF values from all four focus areas predicted from Hyperion (dark) and Sentinel-2 (bright) images in comparison to field samples measured during summer 2012.

If we consider the development of the total amount of available forage at all focus areas, we get an idea of the seasonal dynamics as well as the spatial variability in our research area.

Seasonal dynamics of gBM, ME, and aNDF (**Figure 2.3-10**) were obviously connected to NDVI values and precipitation sums (**Figure 2.3-11**) over the course of the three growing seasons. However, values vary widely between focus areas. Further analysis of the drivers of the development of forage supply revealed that phenology and cumulated precipitation sums over three months exerted by far the most important influence (**Table 2.3-4**).

Figure 2.3-10: Seasonal dynamics of A) total gBM, B) ME and C) aNDF for all four focus areas predicted based on Hyperion time series. Areas affected by cloud cover were excluded.

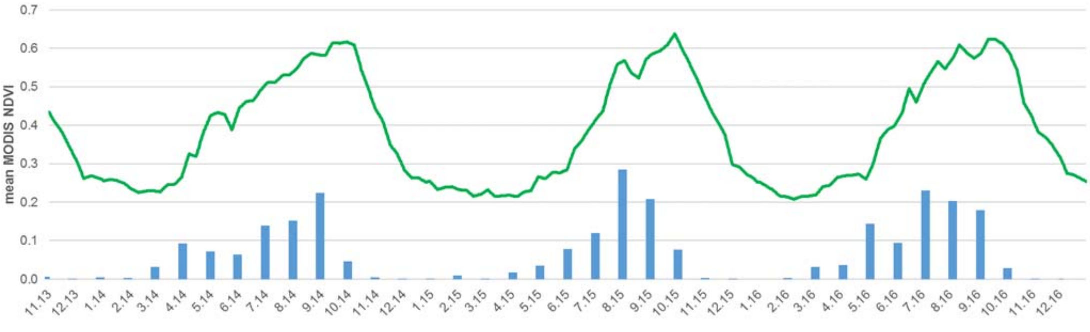

Figure 2.3-11: Seasonal dynamics of MODIS NDVI time series and sum of precipitation averaged over all four focus areas.

Table 2.3-4: Significance levels of predictors chosen by stepwise (forward and backward) selection for each forage characteristic based on Akaike information criterion.

Forage characteristic	Independent variables/predictors					adjR²
	Phenology	Precipitation	cumPrecipitation	Land use	Soil	
Green biomass (gBM)	**		x		x	0.34
Metabolisable energy (ME)	***	*				0.43
Amylase-treated neutral detergent fibre (aNDF)	*		**			0.50
Acid detergent fibre (ADF)	**		*			0.45
Phosphorus (P)	**		*			0.46
Ash (XA)	**		*			0.43

Signifiance codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘x’ 1

Discussion

Performance of resampled forage models – the spectral aspect

For model calibration, we used partial least squares regression due to its ability to deal with the high dimensionality and collinearity of hyperspectral data (Carrascal, Galvan, & Gordo, 2009) while retaining only significant components with a high explanatory power (Harsanyi & Chang, 1994). Moreover, the forage variables considered in this study cover a broad range of different aspects of livestock nutrition. The method applied was successful in calibrating models for gBM, ME, and aNDF for all tested spectral resolutions.

When considering the selected wavelengths, we can find many consistencies between these successful models, which supports the idea of a physical or causal relationship between selected spectral regions and the forage characteristic under investigation (Knox et al., 2012). A comparably lower predictive power was observed for the Sentinel-2 models for ME and aNDF, which can be explained by the missing spectral coverage in the SWIR II region, i.e. only one band is available while the FieldSpec and Hyperion models selected several SWIR II bands for these models. The same can be observed for the model predicting ADF, where the spectral resolution of Sentinel-2 in the SWIR I and SWIR II region is not sufficient. However, without applying further spectral pre-processing techniques, even the full spectral resolution of the field spectroradiometer, but also the satellite resolutions, was not able to successfully model P. In general, P concentrations in the research area are low (Nwoke et al., 2003). Therefore, it might be that spectral adsorption features of more frequent constituents like water, cellulose, and nitrogen might have hindered the detection of P (Kokaly et al., 2009). In addition, inorganic compounds cannot be detected directly via field spectroscopy but only if a correlation exists with detectable organic compounds or structural plant characteristics, which was not found for our dataset (data not shown). Additionally, XA could not be modelled at all since the band selection procedure obviously failed to select meaningful bands.

Even in most models based on hyperspectral data, the algorithm selected only a few bands, possibly due to the high multicollinearity of hyperspectral data (Clevers et al., 2007; De Jong, Pebesma, & Lacaze, 2003). It can be concluded that the low number of broad bands of Sentinel-2 in the SWIR region reduced the predictive power of many forage models in comparison to those based on hyperspectral data (Mansour et al., 2012). However, in general the spectral coverage of Sentinel-2 proved to be sufficiently high and strategically well placed which allows for some important rangeland monitoring and management applications (Sibanda, Mutanga, & Rouget, 2016).

Application of models on satellite data – the spatial aspect

PLSR models have been successfully applied to remote sensing data to produce maps of forage characteristics (Zengeya et al., 2012). We first applied a mask, based on MESMA results, to ensure that models were only applied on vegetation pixels. The idea of such a mask was also realized by Suzuki et al. (2012) and suggested by Coops et al. (2003). In addition, Psomas et al. (2011) ensured during data collection that only pure vegetation pixels were included in their analysis. These examples underline the importance of any preprocessing step that guarantees a match of targets, e.g. vegetation, between model calibration and model application. Here it is not enough to only apply a filter of observed values as a post-processing step, since it can never be assured that the model does not predict reasonable values when applied on incongruous targets, e.g. soil pixels.

Furthermore, for upscaling field-based spectrometric measurements to satellite data, it is mandatory to convert at-sensor radiance to surface reflectance by applying atmospheric correction (Psomas et al., 2011), which will also allow for multi-scene and multi-date analysis. However, due to software limitations, we had to apply two different atmospheric correction methods to Hyperion and Sentinel-2 images, which might have caused some observed differences in pixel values and thus model outcomes (Martin et al., 2008).

Satellite data for monitoring systems – going hyperspectral or multispectral?

When comparing the performance of Hyperion and Sentinel-2, it becomes obvious that none of the tested satellites provides optimal characteristics for the purpose of regular forage supply monitoring in a tropical savanna. Here, we tested Hyperion as a representative of a hyperspectral satellite, since it was the only satellite providing repeatedly and freely available hyperspectral imagery at the time of the study. Even so, we are aware of its major shortcomings, i.e. low signal-to-noise ratio, unpredictable image acquisition, varying image coverage and the fact that the satellite was deactivated on 30 March 2017. The low data quality of the sensor becomes obvious in the grainy model results despite complex image preprocessing. Nevertheless, Hyperion´s spectral resolution led to a higher model fit and lower prediction error for five of the six tested forage characteristics in comparison to Sentinel-2 models, supporting the idea that a higher spectral coverage contains more essential information about plant constituents and thus enables the calibration of diverse and better fitted models for flexible application opportunities (Durante et al., 2014). For future applications, a number of hyperspectral satellites will be available, e.g. PRISMA, EnMAP HyperSpectral Imager, HISUI, Spaceborne Hyperspectral Applicative Land and Ocean Mission (SHALOM), Hyperspectral Infrared Imager (HyspIRI) and Hyperspectral X IMagery (HypXIM) (Transon et al., 2018).

However, until these new satellites are operational, especially for applications in Africa, more practical and affordable multispectral remote sensing alternatives are needed (Zengeya et al., 2012). With the launch of Sentinel-2B on 7 March 2017, an image acquisition every five days is possible, offering optimal conditions for regular monitoring purposes. Also, images from this are freely available. The strategically placed bands of Sentinel 2, especially in the red-edge region, facilitate estimates of chemical constituents and can partly compensate for the reduced data range compared to hyperspectral sensors (Ramoelo et al., 2012).

Nonetheless, the comparison of forage supply maps of multi- and hyperspectral satellites differ considerably. Since predicted data ranges from both sensors fall within the range of the samples taken on the ground, we are not able to determine which satellite provides better estimates although forage maps based on Sentinel-2 data show more realistic patterns. Thus we conclude that another satellite system, combining the advantages of both tested data sources, would be needed to install a more reliable monitoring system. The EnMAP sensor has a great potential to fill this gap in the future. It provides a high spectral coverage (420 to 2450 nm) in combination with a low signal-to-noise ratio at a spatial resolution of 30 m (Guanter et al., 2015). Also, like the Sentinel satellites, it offers a high revisit time of up to four days at the equator as well as cost-free images for scientific use (Guanter et al., 2015). Alternatively, NASA's Hyperspectral InfraRed Imager (HyspIRI) will provide comparably good characteristics for regular forage supply monitoring (Lee et al., 2015).

Drivers of regional forage resources – the ecological aspect

Forage biomass can vary widely in its quality (Huston & Pinchak, 1991) and most animals prefer an intermediate amount of vegetation biomass due to quality quantity trade-offs, i.e. areas with low biomass production are often limited by low ingestion rates, whereas areas with high plant production are limited by the low digestibility of mature forage (Mueller et al., 2008). Therefore it is highly relevant to consider both, the quantity but also the quality of forage resources.

In an attempt to cover two potentially important drivers of forage supply in West African savannas, i.e. climate and land use, our study design captured a gradient of aridity as well as grazing. However, at the broad scale considered in this study, only general conclusions about regional drivers of forage supply can be drawn. In agreement with earlier studies (e.g.Grant and Scholes (2006); Knox et al. (2012)), we found pronounced seasonal changes in forage supply between the wet and dry season. As expected for a dryland region, seasonal dynamics of forage supply are more obviously connected to rainfall patterns than to grazing intensities (Kgosikoma, Mojeremane, & Harvie, 2015).

A general trend observable over the three investigated years is that the driest focus area (Nazinon) as well as the most heavily grazed area (Aniabiisi) tends to provide higher levels of ME. Arid areas support the growth of annual plants (Hempson et al., 2015) which often feature a high forage quality (Le Houérou, 1980). Likewise, intensive grazing pressure in African savannas can induce a shift from perennial to annual plants (Fuhlendorf & Engle, 2001). This supports the idea of aridity and grazing exerting convergent selective forces on plants (Quiroga et al., 2010), e.g. on the dominance of annuals, as found by Linstädter et al. (2014) in an earlier study from African savannas. Furthermore, a shift of plant communities towards highly nutritious "grazing lawns" (Hempson et al., 2015) with a high digestibility (Chaves et al., 2006) and N content (Moreno García et al., 2014) can be observed under intensive grazing impact. High grazing pressure can stimulate the regrowth of fresh palatable plant material (Changwony et al., 2015; Moreno García et al., 2014), thus keeping vegetation at an early phenological stage.

In this regard it is not surprising that phenology, characterized by a progressive decline in digestibility and crude protein (Atta-Krah & Reynolds, 1989; Changwony et al., 2015), was found to be the most important predictor of forage characteristics in the study area. Cumulative precipitation, in contrast to precipitation, integrates the recent history of rainfall events over the last three months. A study in the same research area but at a finer spatial resolution found antecedent rainfall to be an important driver of forage biomass (Guuroh et al., 2018). We assume that cumulative precipitation, in contrast to recent precipitation, is a better proxy of current ground water levels which in turn influence the growth behaviour of forage plants. In addition, cumulative precipitation can modulate the rivers' water levels within our focus areas and thus forage resources of river banks (Nilsson & Svedmark, 2002). These areas are of special importance for pastoralists since they show consistently earlier green-up and delayed senescence and thus act as key pastoral forage sites (Brottem et al., 2014).

An earlier small-scale study of drivers of forage supply, located in the same research area but conducted only during the rainy season, revealed that forage supply is a complex ecosystem service that is mainly directly controlled by land use intensities, i.e. grazing pressure, but also indirect proxies like aridity, vegetation dynamics and weather fluctuations (**Chapter 2.2**). Both studies agree that vegetation dynamics and water availability play an important role in explaining forage supply. However, on the coarser spatial and longer temporal scale of this study, the substantial changes due to the phenological development of plants and the influence of seasonal changes between dry and rainy seasons may have masked the more local influence of land use drivers like grazing pressure.

Limitations of our approach

Our data sampling approach ensured a direct relationship between the spectral reflectance of vegetation and the samples analysed in the lab. However, this was only possible for relatively small sampling plots while other studies have emphasized the importance of a match between field and remote sensing image sampling resolutions (e.g. Thulin et al. (2012)). This approach was not suitable in our case because i) investigated satellites featured different spatial resolutions, ii) an analysis of metabolisable energy is very costly and could not be provided for a representative area of a 30 x 30 m pixel, iii) Hyperion image acquisition was not predictable but depended on weather forecasts, and iv) the flight height and spatial coverage of the Hyperion satellite varied over time.

A further limitation of this approach is that no independent validation of model results was possible and as such, we rely, instead, on an internal cross validation procedure. However, in their crucial study regarding the robustness and transferability of resampled models, Mutanga et al. (2015) found that although model the performance of resampled spectral data tends to overestimate model accuracy in comparison to a real application to satellite data, the magnitude of errors due to the up-scaling procedure is small enough to support a transfer. Therefore, they provide a legitimation of the applied method.

Nonetheless, we emphasise the need to further investigate model performance based on independent validation plots on the ground, which would only be possible for Sentinel-2 models.

Our focus areas differed in features of natural environment, e.g. rivers and forests. Trees can dominate remote sensing based time-series analyses in this area (Brandt et al., 2015), but at the spatial resolution of Hyperion images we were not able to specifically mask out trees. Since leaves provide an important source of forage, especially during the dry season (Ky-Dembele et al., 2016), and the riparian zone provides highly nutritious grasses (Ramoelo et al., 2012) irrespective of the rainy season, we refrained from excluding the whole flood plain. However, our models were specifically calibrated on herbaceous vegetation and an application to pixels dominated by tree spectra might have decreased model reliability in these areas.

Conclusion

While numerous studies have investigated the potential applications of near surface remote sensing in detecting essential chemical constituents of vegetation, few studies have used this method to create maps based on satellite or aerial images in order to tackle urgent ecological challenges. Here, our study presents an attempt to go one step further to directly use remote sensing products, aided by field spectroscopy, in order to determine important drivers of forage supply in an African savanna. Our findings provide evidence that partial least squares regression is able to model several important forage characteristics based on hyperspectral as well as multispectral data. However, generated maps differ considerably: While the high spectral resolution of Hyperion imagery allowed for improved model fits, the better quality of Sentinel-2 images resulted in more realistic maps of forage characteristics. We therefore conclude that so far none of the tested sensors provide optimal features for a regular forage monitoring. In the future, the EnMAP mission will likely fill this gap. Nonetheless, by using a time-series of Hyperion images, we were able to contribute to a better understanding of forage drivers at a regional scale. Future research in this regard should focus on more reliable model validation methods to adequately evaluate model reliabilities before eventually installing automated monitoring systems of forage supply.

3 GENERAL DISCUSSION

Livelihoods of people living in African savannas are intimately linked with this ecosystem, as it provides essential services (Egoh et al., 2009; Marchant, 2010). Rural livelihoods largely depend on livestock (Zaibet et al., 2011) and thus forage is a particularly important ecosystem service (ES) provided by West African savannas. However, spatio-temporal patterns of forage supply are complex (Hiernaux et al., 2009; Wezel & Schlecht, 2004) which makes the implementation of a regular monitoring service a valuable but challenging task.

Linking vegetation attributes to hyperspectral reflectance data by means of field spectroscopy is the first step towards a remote sensing based monitoring of forage resources (Milton et al., 2009). In this context it needed to be tested whether metabolisable energy (ME), as a universal parameter for forage quality, can be modelled by field spectroscopy. Additionally, there is not much experience with the effectiveness of using hyperspectral measurements taken in a tropical region during the rainy season. Finally, the approach to make use of a reduced spectral range ("half-range") of the reflectance curve arises from scientific findings which demonstrate that especially the red and NIR region of the reflectance spectra have a close relationship with relevant plant biochemicals (Biewer et al., 2009b) but the feasibility of this approach for African savanna rangelands still had to be tested.

Understanding the drivers of forage supply in the context of global environmental and climatic change is critical for food security and the implementation of early-warning and monitoring systems (Stuth et al., 2005). As few studies account for combined effects of these global change drivers, we still have a limited understanding of how these drivers jointly shape forage supply (Oliver & Morecroft, 2014; Thornton et al., 2009). Moreover, not many studies aim at disentangling the direct and indirect effects of land-use and climate change on vital ecosystem services provided by rangeland vegetation (Klumpp & Soussana, 2009).

Finally, methodological restrictions impede forage monitoring in tropical savanna systems. Although spectral models have been established using field spectrometer readings resampled to match the band definition of hyperspectral or multispectral satellite sensors (Hansen & Schjoerring, 2003; Shen et al., 2008), only few studies have actually tested to apply these field models to satellite imagery (Leemans & de Groot, 2003; Mistry, 2000). Here, it still remains a challenge to transfer the techniques developed in the field to satellite data. Furthermore, a multitude of different sensors is available but the optimal satellite system to generate regular maps of forage supply of savanna rangelands still needed to be identified (Booth & Tueller, 2003; Hunt et al., 2003).

In this cumulative dissertation I have presented three separate studies addressing different research topics that all conduce to a common goal, i.e. to enable a regular knowledge-driven and satellite-based determination of forage quality and quantity in an African savanna (**Figure 1.6-1**). All of my studies have successfully contributed to this goal and addressed urgent research gaps: In my first study – “Spectral models of forage supply” – I was able to show that not only forage quantity, i.e. green biomass, but also forage quality, i.e. metabolisable energy content, could be successfully modelled by means of near surface remote sensing techniques in combination with partial least squares regression. Even under the very difficult measurement conditions in a tropical region during the rainy season, robust and transferable models could be calibrated using full-range spectral data. Models using only half-range data still rendered satisfactory results.

Subsequently, I made use of the best performing spectral models by applying them to a variety of different rangeland types to estimate forage supply. These data were used for the second study “Drivers of forage supply in savanna ecosystems”. By combining the advanced statistical method of structural equation modelling (SEM) within the well-defined framework of social-ecological systems (SESs), I was able to determine that mainly land-use, but also short-term vegetation dynamics and weather fluctuations, are the most important drivers of forage supply in the research area. In contrast, climate exerted mostly indirect effects via land-use drivers.

Building on these insights, as well as upscaling and further adapting the remote sensing tools of the first study, I was eventually able to propose a methodology for a satellite-based monitoring of forage resources within the scope of the third study “Model application for forage monitoring”. Results indicate that neither of the both tested satellite systems, i.e. the hyperspectral satellite Hyperion as well as the only recently launched multispectral satellite Sentinel-2, feature optimal qualities for forage monitoring purposes. Nonetheless, I could demonstrate the usefulness of the generated forage maps by using them for an analysis of drivers of forage supply at the regional scale. Here I could integrate the knowledge of drivers at the plot and site level of the second study.

In the light of all acquired findings, there is a need for a critical discussion of the applied study approaches and the validity of the obtained results.

3.1 SPECTRAL MODELS OF FORAGE SUPPLY

In the first study of this thesis, I compared full-range and half-range spectral models predicting the vegetation’s metabolisable energy (ME) and green biomass (gBM) content based on the vegetation´s reflectance.

Robust validation of spectral reflectance models

All presented spectral models were validated using two different methods. Firstly, I applied an adapted cross-validation approach, successively pertaining to one of the 21 sites used for data collection. This approach was meant to mitigate any possible effects of spatial autocorrelation. Secondly, I applied a one hundred times repeated cross-validation by randomly excluding 25% of all data points. The intention of applying two different validation methods was to ensure model robustness. However, subsequent model applications on vegetation reflectance data measured within our research area revealed that models without further preprocessing steps tended to estimate more realistic target variables than preprocessed models (using derivative calculations). Hence, I assume that unprocessed models were more robust under the extremely difficult measurement conditions, such as high air humidity, almost constant cloudiness with rapidly changing illumination conditions and, most importantly, a sparse vegetation cover (Fensholt et al., 2004; Gessner et al., 2013). This observation is in contrast to our validation results (Ferner et al., 2015) as well as other literature findings (e.g. Demetriades-Shah et al. (1990); Thulin et al. (2012); Tsai and Philpot (1998)) reporting enhanced model performances by applying derivative calculations. I assume that my models, preprocessed by derivative calculations, tended to be overfitted (Babyak, 2004) despite all countermeasures (see validation procedure). This implies that not the models with the best results in the validation procedure actually predicted the best fitting forage variables, presumably because these models incorporated irrelevant predictors (Hawkins, 2004), e.g. random noise.

Consequently, I decided to use only unprocessed models for all further applications with the additional advantage of a better comparability between these models and those adapted to satellite resolutions. Here, applying models using derivative calculations would have led to the problem of only minor comparability due to a different number and distribution of bands as well as different noise behaviour of spectral data (Mutanga et al., 2015). I conclude that, especially under difficult measurement conditions, an independent validation dataset is increasingly important but could not be used in this study as the number of available samples was too low (due to spoiled samples and difficult logistics in the research area).

3.2 DRIVERS OF FORAGE SUPPLY IN SAVANNA ECOSYSTEMS

The aim of the second study presented here was to determine important drivers of forage quality and quantity in African dryland rangelands within a SES framework. Forage quality (ME) of sampled plots was estimated by applying spectral models (without derivative calculations) calibrated within the scope of the first study. By applying SEM, the significance of a variety of drivers affecting the target forage variable was determined.

Missing drivers for forage quality

Data on forage quality is seldom available for large areas or numerous sample points due to high costs and sampling demands (Pullanagari et al., 2012), which underlines the importance and scientific value of my results. However, with 45% of variance explained, model fit for the SEM model of ME was comparably low. I assume that our path model did not include some important drivers of this complex forage variable. Most importantly, biotic parameters like plant species (Hughes et al., 2013a) and leaf-to-stem ratio (Ball et al., 2001; Hare, Tatsapong, & Phengphet, 2009) will alter forage quality but could not be considered here. Also, the grazing history might have had an important influence on forage quality as well as inter-site variation in tree and shrub densities (Turner, 1998a, 1998b).

Potentially important abiotic factors not included in the model were flooding (Durante et al., 2014) and other extreme habitat conditions. In this regard, Nacoulma et al. (2011) indicate that grazing often takes place at particularly unfavourable microsites being e.g. too dry, wet or rocky for agriculture.

Lastly, ME values were estimated from spectral data and can thus be influenced by varying soil cover or leaf morphology, which can impact foliar optical properties (Monje & Bugbee, 1992). However, tropical grasses are often of low nutritive quality (Adu & Adamu, 1982) so that the small range of ME values in the research area alone might have hindered a better model fit.

Non-linear variable responses

I used SEM to disentangle the importance of various drivers within the social-ecological system of dryland rangelands. Path models are a powerful and flexible tool to simultaneously analyse several relationships within a linked network (Sanchez, 2013). Besides, they can represent and thus ease an understanding of hypotheses and theoretical concepts in causal networks (Grace et al., 2010). Although SEM is comparatively robust regarding measurement scales, sample size, and residual distribution (Wold, 1985), one drawback is that no non-linear relationships can be properly captured without further adjustments. Savadogo et al. (2007) for example found a non-linear response of vegetation cover to increased grazing intensity. However, I plotted correlograms of all variables previous to model calibration and did not find any clear non-linear relations in my dataset. Therefore I assume SEM to be an appropriate statistical method to attain the study aim.

Direct and indirect effect pathways

A further crucial advantage of SEMs is their ability to separate between direct and indirect effects on the target variable. Thus I was able to identify some divergent pathways within my SESs compared to the original framework by Stafford Smith et al. (2007), i.e. direct pathways from social and external drivers to the ecosystem service of forage supply. There are two possible explanations; one reason might be that I did not adequately depict processes and drivers within the ecological subsystem that initiate the response on forage supply, e.g. tree cover (Allred et al., 2012). However, it might also be possible that drivers can directly affect the ecosystem service of forage supply due to their very direct temporal response (cf. **Table 2.2-1**). Here, management tools (e.g. grazing) can act as direct disturbances by removing plant biomass while external effects (e.g. soil moisture) can cause an immediate effect, e.g. by rehydrating plant material (Westoby, 1979). Here I found a temporal scale mismatch between the effect of drivers and the response of the ecological subsystem (Cumming, Cumming, & Redman, 2006). To also capture these short-term effects, one would have to cover very different hierarchical levels of vegetation response, from individual physiological and/or metabolic responses to broad changes on ecosystem structure and function (Smith, Knapp, & Collins, 2009), which clearly reach beyond the scope of the present study.

3.3 MODEL APPLICATION FOR FORAGE MONITORING

In the course of the third study, statistical models from the first study were resampled to multi- and hyperspectral satellite resolution to create maps of forage supply for the research area.

The value of maps as a scientific output

It is an important step for scientists to not only calibrate robust spectral models based on field spectroscopy but to use the knowledge gained to eventually create maps, thus generating important spatial information (Lawrence, Wood, & Sheley, 2006). Although valuable knowledge can be gained by field based models, one should keep in mind that even in industrial countries a regular use of a field spectroradiometer, especially a full-range device, is limited to a small number of people, in particular scientists. However, people that would benefit most from regularly available forage estimates would be farmers and livestock-keepers, which would need spatial information of vegetation properties for informed management decisions (Pullanagari et al., 2016).

It can be concluded that the most practical usage of my spectral models is the application to air-borne or space-borne imagery to create maps that could eventually be provided to end-users. This would also allow an application of this high-end technology for users in developing countries. Despite limited access to many modern technologies, mobile phones are very common (Aker & Mbiti, 2010). It would thus be possible to distribute information gained by the presented research project, i.e. the spatial distribution of valuable forage resources, to pastoralists and farmers via mobile phones.

Since sedentary farmers have only limited options to adapt their feeding behaviour according to this information, the greatest benefit would be expected for pastoralists that can, within a certain range, modify their transhumance movements accordingly (Brottem et al., 2014). Hereby it might be possible to avoid unnecessary conflicts between both groups (Turner et al., 2012). In addition, an overexploitation of forage resources by unregulated and non-adapted grazing behaviour could be reduced (Amiri & Shariff, 2012). Lastly, animal performance and survival rates will be enhanced if high quality forage and/or heavyset forage resources can be offered to the animals (Grant & Scholes, 2006).

4 GENERAL CONCLUSION

The overall findings of the present dissertation provide an important step towards a regular monitoring service of forage supply within a tropical savanna. The study provides an integration of tools at the plot level and the regional scale as well as a profound understanding of the mechanisms driving forage quality and quantity.

An exceptional component of the presented study is the selection of the study area featuring a steep regional climate gradient. This set-up allowed for an investigation of climate change impacts on forage resources in a flexible way, i.e. by covering more humid areas that correspond to analogous climates for the WASCAL core research sites (**Box 1.4-1**), as well as more arid areas since climate projections for Africa vary widely (Hulme et al., 2001). Additionally, the study area featured steep local gradients of land-use pressure thus presenting a crossed space-for-time substitution which allowed for disentangling these two major components of global environmental change (Oliver & Morecroft, 2014).

A novel aspect of the presented study is the consideration of metabolisable energy, determined by *in vitro* gas production, as a meaningful parameter of forage quality, reflecting the real “profit” of forage for the animal (Getachew et al., 1998). Many studies and discussions neglect the importance of the quality of forage. This is especially short-sighted in the context of savanna vegetation, often featuring very low nutritional values, specifically during the dry season (Atta-Krah & Reynolds, 1989). Under these situations, voluntary intake and digestion rates are dramatically reduced (Ball et al., 2001) which might cause starvation of ruminants.

However, while laboratory analyses using the Hohenheim gas test are extremely costly and time-consuming (Schenkel, 1998), the application of field spectroscopy to estimate ME offers numerous new possibilities to answer urgent scientific questions. I chose to make use of this technique to unravel important direct and indirect drivers of forage supply in dryland rangelands and thus contribute to a better understanding and hence better management of this vital resource (Guuroh et al., 2018).

Understanding the complex interactions of drivers of forage supply in the context of global environmental and climatic change supports the interpretation of future forage monitoring products which helps to produce user-friendly and user-useful outputs for various stakeholders (Pierce et al., 2005). However, few studies have investigated the combined effects of these important drivers of global change before (Oliver & Morecroft, 2014; Thornton et al., 2009). Here I was able to disentangle some of the complex interactions of land-use, external/climatic and ecological drivers on forage supply. These findings provide important insights for the establishment of mitigation measures against global change (see Guuroh et al. (2018)) and to upscale and predict global change effects on forage supply (Campbell et al., 2000).

Moreover, I contributed further arguments to the climate vs. grazing “impasse” (Archer, 2004; Turner & Hiernaux, 2002) by showing that the way humans use dryland rangelands has a greater implication on forage supply than aridity itself. This result highlights mankind’s responsibility as well as possibilities to combat climate change.

Finally, by subsequently developing a straight-forward application based on my initial results, it was possible to map forage supply in space and time and to create maps, which could allow farmers and pastoralists to better manage livestock keeping (Brottem et al., 2014). Furthermore, the generated maps represent an easy to understand and distribute medium that can ease the dialog between the scientific world and wider society (Whittaker et al., 2005) and it is a great example for a directly usable output of scientific research.

In this regard, I was able to compare two very interesting satellite systems. Hyperion on the one hand was, to date, the only hyperspectral satellite with more than 100 bands regularly providing data free of charge (Nagendra & Rocchini, 2008). Sentinel-2, on the other hand, was only recently launched so that the provided images have not yet been intensively tested for savanna rangeland applications, which makes my results an important scientific contribution.

As the Sentinel satellites within the Copernicus programme represent the new flagship of the European Space Policy, being one of the most ambitious and comprehensive Earth-monitoring programmes ever (Butler, 2014), these results will presumably attract wide interest.

Another novel aspect of my study is the coherence of my key method, i.e. PLSR. On the one hand, I applied hyperspectral forage models in the field to generate data of forage supply at the plot-level over two consecutive growing seasons. On the other hand, I adapted the same models to be used on satellite data to generate forage estimates at the spatial resolution of single pixels, i.e. 10 m and 30 m, respectively, at the spatial extent of several watersheds and over several years. Thus, a rare opportunity is provided to compare coherent scientific findings from different spatial and temporal scales, which gives important information about the transferability of these results (De Knegt et al., 2010; Freckleton, 2004). Here, a first initiative was taken by comparing drivers of forage supply at different spatial scales, but further studies of scale-dependency of ecological processes are possible which could be looked into in more detail in future research studies.

However, my doctoral thesis can only contribute towards a future regular automated monitoring system of forage supply but does not yet provide the means to install one. Further research is needed to answer the remaining open questions. One aspect is an independent validation of spectral models of forage supply based on in-situ hyperspectral reflectance. Due to the challenging measurement conditions in a tropical savanna during the rainy season, the uncertainty of models for real-life applications should be verified based on independent vegetation samples. Also, further research is needed to better understand the factors that modulate forage quality in the research area at a fine spatial scale. As illustrated above, metabolisable energy is a forage characteristic of special importance but could not yet be modelled with satisfactory accuracy although I was able to sample data from two growing seasons. However, the main pending issue remains regarding a ground based validation of forage supply maps, which should most reasonably be done when appropriate hyperspectral satellites like EnMAP become available (Transon et al., 2018).

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Table A - 1: Overview of predictor (latent) variables for structural equation modelling (SEM), sorted by driver/response types (**Table 2.2-1**). The associated indicators (and sources) used to model forage provision (ME, tBM, MEY) are also listed. Please note that information is derived at different scales; if not indicated otherwise, data is acquired at site (village) level.

Latent variable	**Drivers of the social subsystem (S)**
	Indicator 1
Grazing	**Grazing pressure** Estimation of grazing pressure at plot level from 0 = very light to 4 = very heavy (Linstädter et al., 2014).
Fire	**Fire Frequency** Data on fire events from 1st November 2008 to 31st October 2013 were acquired from MODIS Active Fire Detections extracted from MCD14ML distributed by NASA FIRMS (Available online at https://earthdata.nasa.gov/active-fire-data). Fire events were normalized by calculating fire frequencies per km² and year at each site from a 5 km buffer around the village centre.
Protection	**Protection status** Protected areas as defined by IUCN and UNEP-WCMC (2013), including Gonse and Nazinga (classified forests) in Burkina Faso and Mole (national park) in Ghana.

Latent variable	External drivers (X)						
	Indicator 1	Indicator 2	Indicator 3	Indicator 4	Indicator 5	Indicator 6	Indicator 7
Aridity	**Climate zone** The investigation area was separated into three zones based on isohyets (>1000 mm = zone 1, 800-1000 mm = zone 2, <800 mm = zone 3).	**Aridity index** UNEP aridity indices (Middleton & Thomas, 1997) were calculated based on WorldClim (Hijmans et al., 2005) climate data.	**Pot. evapotranspiration [mm day^{-1}]** Monthly averages of potential evapotranspi-ration over the period 1950-2000 were extracted from CGIAR-CSI Global-Aridity and Global-PET Geospatial Database (Trabucco & Zomer, 2009).	**Temperature seasonality** Standard deviation*100; from WorldClim (Hijmans et al., 2005) climate data.	**Mean annual precipitation [mm]** Data from WorldClim (Hijmans et al., 2005) climate data.	**Precipitation seasonality** Coefficient of variation; from WorldClim (Hijmans et al., 2005) climate data.	**Precipitation of driest quarter [mm]** Data from WorldClim (Hijmans et al., 2005) climate data.
Soil moisture	**Soil moisture [%]** Data from day of measurement from NASA LPRM/TMI/TRMM Daily L3 Day Surface Soil Moisture (Owe et al., 2008) derived from passive microwave remote sensing data from the Tropical Rainfall Measuring Mission (TRMM) Microwave Imager (TMI), using the Land Parameter Retrieval Model (LPRM). If necessary, data was interpolated by spatio-temporal interpolation using R package "spacetime" (Pebesma, 2012).	**Accumulated soil moisture [%]** See **Soil moisture**; data was summed up over three days (two days before data collection and day of data collection)					

Latent variable	Drivers of the ecological subsystem (E)	
	Indicator 1	Indicator 2
<u>C4 plants</u>	**Relative biovolume of plant species with C4 photosynthesis pathway [%]** Based on vegetation relevées (Guuroh et al., 2018), the relative biovolume of plant species with C4 photosynthesis pathway (averaged per plot) was calculated.	
<u>Degradation state</u>	**RESTREND** Global Residual Trend of Sum NDVI (RESTREND) 1981-2003 published by UN FAO via GeoNetwork. Wessels et al. (2007) proposed a method to avoid the correlations between rain-use efficiency and rainfall to better distinguish land degradation from the effects of rainfall variability. First, a regression between observed sum NDVI (measured by Advanced Very High Resolution Radiometer (AVHRR)) and rainfall was established for each pixel, i.e. a model predicting sum NDVI using rainfall data. The model´s residuals (i.e. differences between observed and predicted sum NDVI) for each pixel were extracted and analysed by linear regression. In our study, only negative trends were considered (i.e. only degradation not recovery).	
<u>Legumes</u>	**Relative biovolume of leguminous species in vegetation clusters [%]** Based on vegetation relevées (Guuroh et al., 2018), the relative biovolume of leguminous plant species (averaged per plot) was calculated.	
<u>Perennials</u>	**Relative biovolume of perennial plant species [%]** Based on vegetation relevées (Guuroh et al., 2018), the relative biovolume of perennial plant species (averaged per plot) was calculated.	
<u>Phenophase</u>	**Phenology** Based on species-specific biovolume and phenological stages, community-weighted phenology was calculated at subplot level and averaged at plot level (Guuroh et al., 2018). Phenology values are 1 = Shooting, 2 = Sprouting, 3 = Flowering, 4 = Fruiting, 5 = Senescent.	

Slope	**Slope position** Slope position along topographic transect, i.e. lowland (1), footslope (2) and upslope (3) (Guuroh et al., 2018).	
Soil fertility	**N content [%]** Result of soil analysis at plot level (Guuroh et al., 2018).	**C content [%]** Result of soil analysis at plot level (Guuroh et al., 2018).
	Ecosystem services (ES) **Indicator 1**	
Forage quality	**Forage quality [MJ kg^{-1} DM]** Metabolisable energy (ME) estimated from spectral reflectance data of vegetation using a statistical model calibrated in the same research area (Ferner et al., 2015).	
Forage quantity	**Forage quantity [g m^{-2}]** Total biomass (tBM) estimated from height and cover values of plant species using a statistical model calibrated in the same research area (Guuroh et al., 2018).	
Forage ME yield	**Forage ME yield [MJ kg^{-1} DM]** Combination of forage quality and quantity (MEY) calculated by multiplying ME and tBM and dividing by a factor of 1000.	

Table A - 2: The conceptual path model in the form of an interaction matrix indicating all pathways between drivers that remain in SEM after applying the defined rule set based on expert knowledge. The matrix is read as “columns affecting rows”; i.e. a cross in the cell x; y (x-th column and y-th row) means that column x could affect row y. Since no driver can affect itself, the diagonal of the matrix is empty. The cells above the diagonal are also empty since SEM is a recursive model (no loops are allowed within the inner model).

	Aridity	Slope	Protection	Soil moisture	Grazing	Fire	Degra-dation	Soil fertility	Pheno-phase	C4 plants	Legu-mes	Peren-nials
Aridity												
Slope												
Protection												
Soil moisture												
Grazing	X	X	X									
Fire	X		X		X							
Degra-dation	X		X		X	X						
Soil fertility	X	X	X		X	X	X					
Pheno-phase					X							
C4 plants	X	X	X		X	X	X	X				
Legumes	X	X	X		X	X	X	X		X		
Perennials	X	X	X		X	X	X	X		X	X	

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