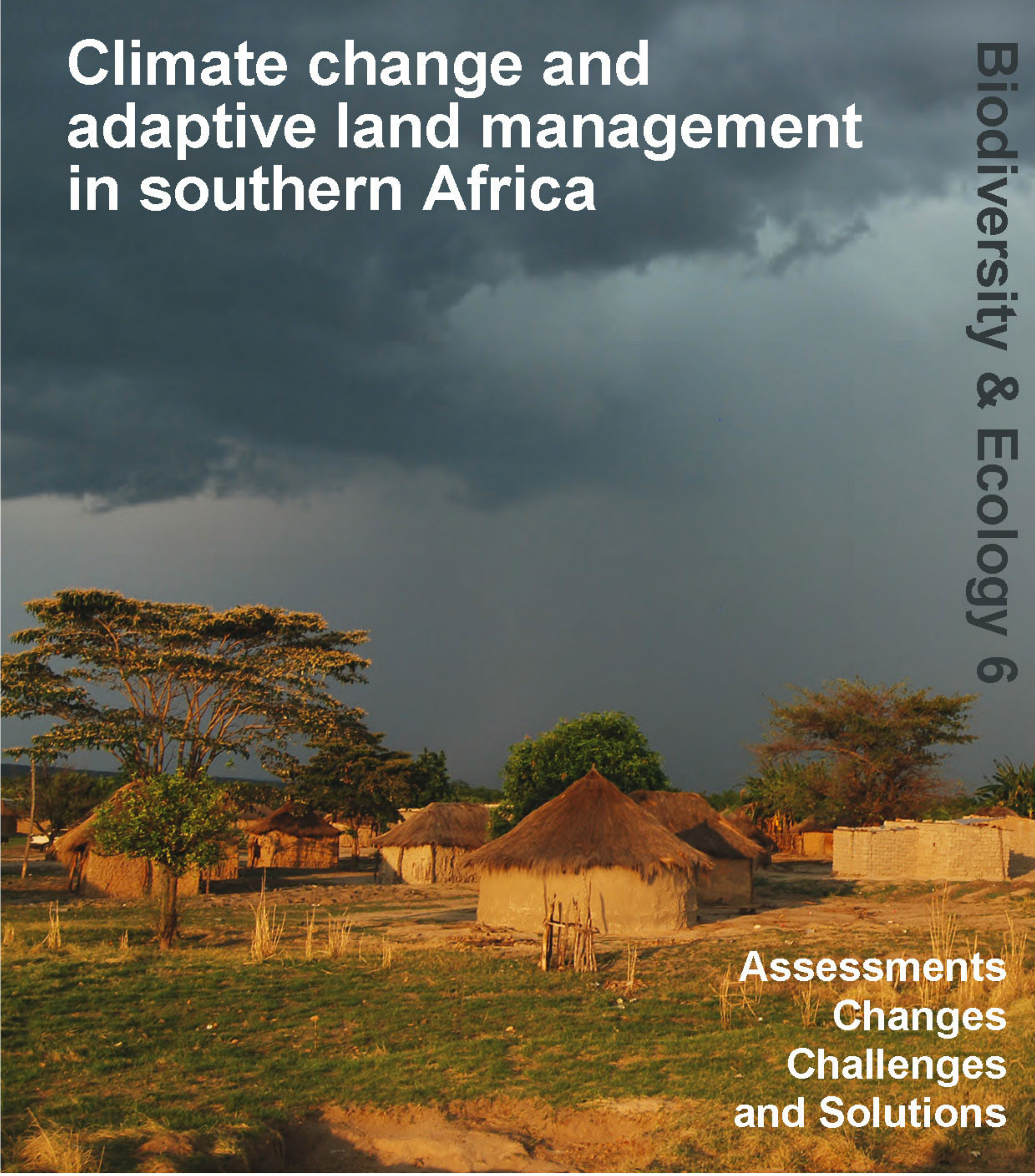
Climate change and adaptive land management in southern Africa

Biodiversity & Ecology 6



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Changes
Challenges
and Solutions

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Climate change and adaptive land management in southern Africa

Assessments, changes, challenges, and solutions

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Forage quality and availability for large herbivores in southern African rangelands

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Abstract: In light of the growing human population, the pressure on herbivores (livestock and wild herbivores) will be accelerated, resulting in a need for effective land management. To achieve this, information and knowledge about the availability and quality of food resources of large herbivores and possible changes in those resources are a prerequisite. In this chapter, we will summarize different projects conducted regarding food availability and quality within SASSCAL. We will give an example of the use of remote sensing as an effective tool for measuring food availability and quality on a large scale. Here, we visualize changes in leaf nitrogen concentration and annual grass biomass. In two other projects, we studied different aspects of plant response. In a fence-line study, we investigated the influence of overgrazing on the plant quality of grasses. Though we detected positive impacts on plant quality, but due to high grazing pressure, the reduction in biomass resulted in an overall decline in the quality of the overgrazed site. In the other project, we tested the plant response of bush encroacher species to damage by herbivores. In contrast to the grasses of the fence-line study, in the shrub species we observed a tendency for reduced protein concentration. The reduction varied among the different plant species, but it did not have consequences on subsequent consumers (Boer goats). In our last project we focused on the impact of increased temperature and reduced humidity on the plant quality of five grass species. Here, we found a species-specific response. We conclude the article with a synthesis and an outline of possible management implications derived from the different studies.

Resumo: Devido ao crescimento da população humana, a pressão nos herbívoros (gado e herbívoros selvagens) irá acelerar, resultando na necessidade da gestão efectiva da paisagem. Para atingir este objectivo, é necessário informação e conhecimento sobre a disponibilidade e qualidade dos recursos alimentares de grandes herbívoros, e possíveis alterações. Neste capítulo, resumimos diferentes projectos realizados dentro do tópico da disponibilidade e qualidade de alimento no contexto do SASSCAL. Daremos um exemplo de detecção remota como uma ferramenta útil para a medição da disponibilidade e qualidade do alimento em grande escala. Aqui, visualizamos alterações das concentrações de azoto foliar e da biomassa anual das gramíneas. Em dois outros projectos, estudámos diferentes aspectos da resposta de plantas. Num estudo de cercas, investigámos a influência do pastoreio excessivo na qualidade das ervas. Por um lado, detectámos impactos positivos na qualidade das plantas. Porém, por outro lado, a reducção da biomassa resultou num declínio geral da qualidade do local sobrepastoreado. No outro projecto, testámos a resposta de espécies invasoras lenhosas aos danos provocados por herbívoros. Ao contrário das gramíneas do estudo de cercas, observámos uma tendência para a redução da concentração de proteína nas espécies arbustivas. A redução variou entre as diferentes espécies de plantas, mas não teve consequências nos consumidores subsequentes (cabras boer). No nosso último projecto, focámo-nos no impacto do aumento da temperatura e redução da humidade na qualidade de cinco espécies de gramíneas. Aqui, descobrimos uma resposta específica da espécie. Concluimos o artigo com uma síntese e descrevemos possíveis implicações de gestão derivadas dos diferentes estudos.

General introduction

The extraordinary impact of large herbivores on terrestrial ecosystems has already been pointed out in the overview chapter on rangelands (Ramoelo et al., 2018). A growing human population will lead to more intense use of landscapes, including increased demands for meat satisfied by either a growing number of livestock or higher hunting rates for wild herbivores (so-called bush meat). As a result of different factors, however, land degradation has become a severe threat, especially in areas that depend on livestock and game farming (Lehmann et al., 2009). An accelerated habitat loss for wild animals and pasture loss for livestock is projected for vast areas of southern Africa (Harris et al., 2014). All forms of land degradation lead to a reduction in or loss of urgently needed food for herbivores and additionally to a decline in the biodiversity of food plants (Harris et al., 2014; Murphy et al., 2016). Especially in areas with high seasonality, food availability changes rapidly and is highly related to annual rainfall, especially for grasses. To help monitor changes in food availability, remote sensing measuring techniques are a useful tool to provide us with data about food availability and quality on a large scale to manage the distribution of large herbivores, especially for wild-ranging herbivores and cattle. Nevertheless, herbivores' food selection is difficult and driven by various factors. For instance, our understanding of quality might not match the understanding of quality by a specific herbivore. For financial, technical, and logistical reasons, we tend to simplify feeding decisions in our efforts to manage the complex interactions and feeding systems of different herbivores and the plant response driven by feeding.

In the following we will give a short introduction of general nutritional concepts, feeding strategies, and the term *quality* as it relates to feeds, with a specific emphasis on ruminants, and then proceed to present different examples of our work.

Surrounded by a multidimensional feeding environment (as described in the overview chapter, Ramoelo et al., 2018), every animal has to search for the optimal food to obtain appropriate quantities of required nutrients, which usually vary by species. These nutrients are proteins, fat, carbohydrates, and to some extent minerals and vitamins. Moreover, an individual's underlying nutritional need varies not only with internal factors (e.g., age, body size, physiological aspects, life stage) but also with external factors such as weather conditions and season (see, e.g., Barboza et al., 2008; Robbins et al., 1987; Van Soest, 1994). Therefore, different individuals even within one species may select different types and amounts of food.

One of the biggest obstacles in our understanding of the food selection of herbivores, however, is that nutrients are available not as single item in one feeding bout but in a mixture of different items in one bite. For example, a high protein concentration in a food plant might be linked with high concentrations of toxic alkaloids (a group of plant secondary metabolites [PSMs]) or anything else. Therefore, animals most likely do not maximize one nutrient currency (e.g., select only one plant species as food because of its high nitrogen concentration) but instead balance their diet among different plant compounds not only to satisfy their nutritional needs (nutrient balancing; see Felton et al., 2016; Simpson & Raubenheimer, 2012; Westoby, 1974) but also to avoid negative effects such as toxification by PSMs (Freeland & Janzen, 1974) or over-ingestion of nutrients, which can also lead to detrimental health issues for the animal (Deutz et al., 2009; see also the info-box 'What Is Quality for a Ruminant?', Stolter et al., 2018). This balancing act is often reflected by the ingestion of a high variety of food plants (so-called diet-mixing [Villalba et al., 2002]), which can be fulfilled only in a heterogeneous, diverse environment.

Different feeding strategies to exploit different food plants have resulted in morphological and physiological adaptations in herbivores. As ruminants are the most important group of herbivores to humans and also the largest group of wild large herbivores, we will focus on their food adaptations. Note that other animals (e.g., hindgut fermenters such as elephants and zebras) differ in their adaptations and will therefore differ in their food selection and their ability to digest specific food items. Because of differences in feeding strategies and consequently differences of the gastrointestinal tract, ruminants are subdivided into feeding guilds (nutritional phenotypes) defined by their favoured food: grazers (grass and roughage feeders), mixed-feeders (intermediate type) and browsers (concentrate selectors; e.g., Clauss et al., 2008; Hofmann, 1989). The classification of these guilds is not family-specific (e.g., bovids occur in all feeding guilds, and 'grazer' does not mean that the animal feeds exclusively on grass). Interestingly, as a consequence of differences in the chemistry of food plants ingested (grasses or herbs and trees), these feeding guilds can also be arranged in an order reflecting their ability to cope with PSMs, the so called avoidance–tolerance continuum, from grazers (lowest in tolerance) to browsers (higher in tolerance; Iason & Villalba, 2006).

In contrast to other animals, ruminants have developed a unique complex digestive system that enables them to live exclusively on plants. This ability makes ruminants favourable for domestication as they can convert indigestible plants into valuable products (e.g., meat, milk) for humans. A community of different symbionts (microbiome) located in the rumen foregut is responsible for the digestion of plant material that is indigestible to non-fermenting animals, as ruminants themselves do not produce enzymes to degrade typical plant compounds like cellulose (Stevens & Hume, 1998). By fermenting plant material, the microbiome provides its host with essential energy in the form of short-chain fatty acids (Van Soest, 1994) and, as soon as the symbionts flow out of the rumen, with an additional source of protein (Hofmann, 2010). Hence, in contrast to other animals, a ruminant lives only indirectly on the food ingested, depending to a great extent on what is provided from the symbiotic community. Therefore, feedback loops from its microbiome might be necessary for a ruminant to learn which food to ingest and which to avoid (Provenza, 1995). This diet-related microbial community is complex and has coevolved with food plants over millions of years.

We found different microbial communities and differences in their function in different herbivores adapted to the food they usually ingest (e.g., grasses, forbs, browse; Mao et al., 2013; Petri et al., 2013). Therefore, it is a challenge to determine the quality of food for large herbivores, as these animals are highly adapted to their natural food. Hence, our point of view on quality is driven mainly by overall general patterns but might not necessarily fit to the preferred food of a given herbivore (see also 'What Is Quality for a Ruminant?', Stolter, 2018).

In the following sections we will provide extended summaries of different projects conducted within different tasks of SASSCAL. We will focus not only on remote sensing as a useful tool for measuring food availability and quality on a large scale but also on the impact of human land management as well as the influence of climate change on these topics. The projects are not directly related and rather show different aspects of the main topic of food availability and quality.

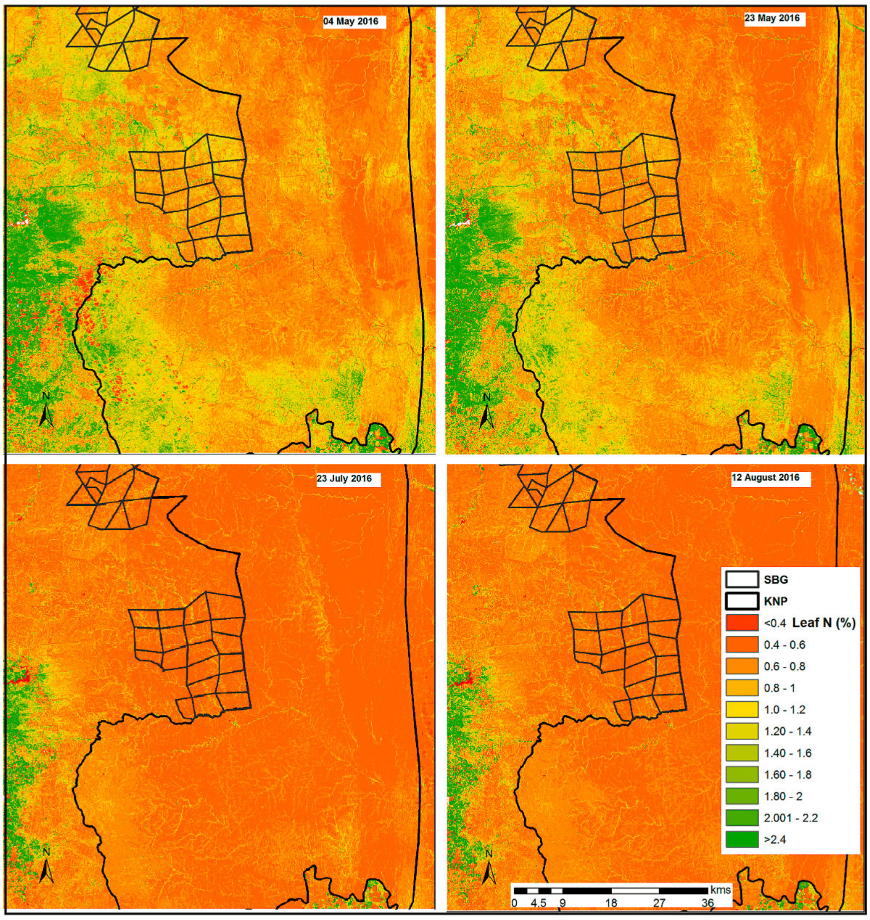

Figure 1: Spatial distribution of leaf nitrogen concentrations (%) as an indicator of grass quality in the Kruger National Park (KNP) and Sabie Sands Game Reserve (SGB) area (Ramoelo & Cho, 2018).

A. Remote sensing to estimate forage availability and quality projects

Introduction

Why is it important? Forage availability assessment is important to understand the state, extent, and quality of rangeland ecosystems. There are several indicators used to measure forage quantity and quality, of which biomass (mass per unit area) and grass or forage nitrogen (forage N) concentrations (indicator of protein content — that is, percentage of dry matter) are commonly used indicators. Forage quality and availability influence the movement and feeding patterns of herbivores including livestock (Ben-Shahar & Coe, 1992; Kaszta et al., 2016). A rapid increase in human population could result in land cover and land use changes that could continue to distress rangelands and food security through land degradation (FAO, 2010; Thornton, 2010). Land degradation is regarded as a threat to the productivity of rangelands (FAO, 2010). Degradation or loss of rangeland potential to provide grazing resources is also exacerbated by the ongoing global climate change phenomenon (Palmer & Bennett, 2013). Climate change induces erratic rainfalls and increases temperatures. As a result, disasters such as drought become prominent in Africa, affecting a high proportion of livestock production by reducing the availability and quality of grazing resources. Assessment of the quality of rangelands could provide information to inform decision-makers on planning and management. As an example, we visualized changes in leaf nitrogen concentration and annual grass biomass in the Kruger National Park between different seasons and years.

Methods

Assessment of forage availability and quality can be assessed using in situ or field-measured data. Remote sensing provides an alternative approach for mapping forage N and biomass for wider geographic areas and over time. The estimation of leaf N in grass has been successful using hyperspectral data derived from field spectrometers, airborne data (Knox et al., 2012; Mutanga & Skidmore, 2004; Ramoelo et al., 2013; Skidmore et al., 2010), and satellite remote sensing (Ramoelo et al., 2012; Ramoelo et al., 2015a). The mapping of forage N is possible because of the development of the second generation of vegetation indices based on the red edge wavelength, known to be positively related to chlorophyll and N (Cho & Skidmore, 2006; Curran et al., 1991) and narrow band indices (Mutanga & Skidmore, 2004; Mutanga & Skidmore, 2007; Ramoelo et al., 2012; Ramoelo et al., 2015a; Ramoelo et al., 2015b). Satellite sensors such as WorldView-2, RapidEye, and Sentinel-2 (freely available) have been successfully used to map grass N, and grass biomass has been successfully mapped since the 1970s using Landsat and, recently, MODIS sensors. Empirical regression analysis is often used to relate in situ measured grass N and biomass with vegetation indices derived from remote sensing images to create prediction

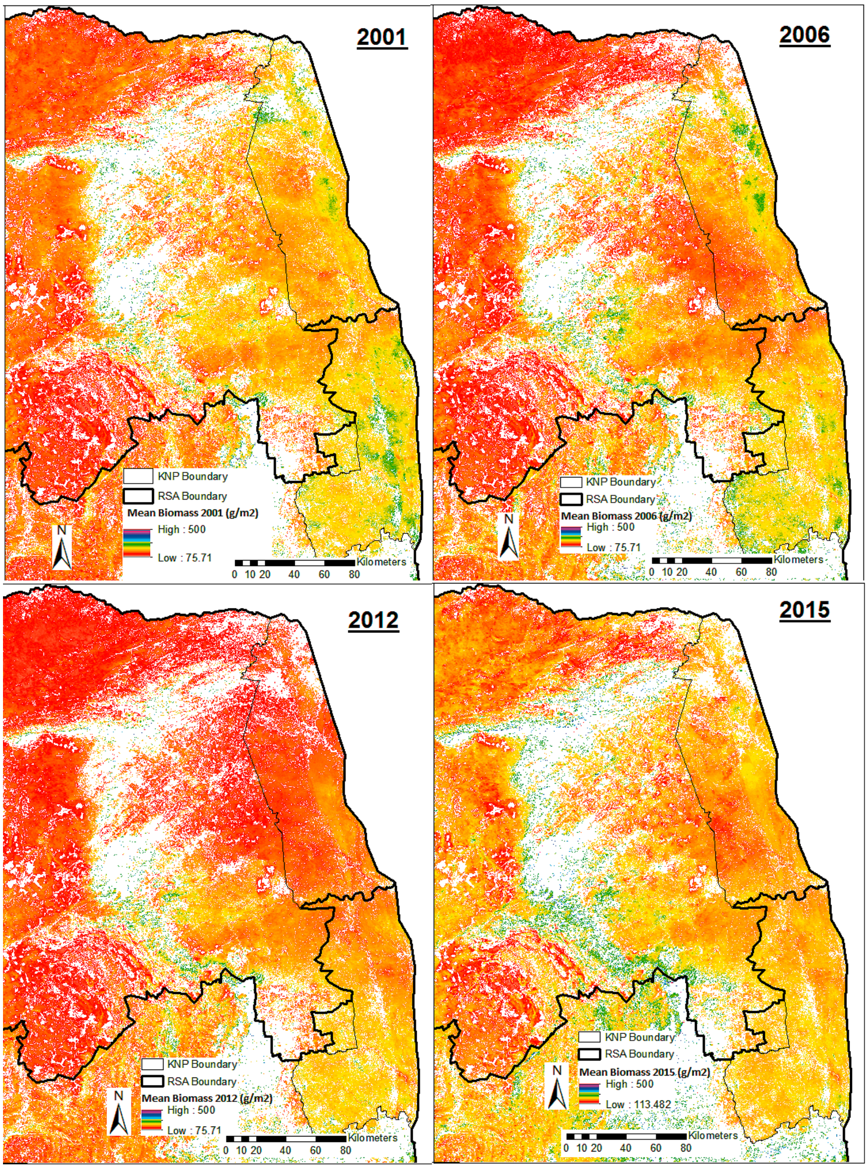

Figure 2: Spatial distribution of mean annual grass biomass (g/m2) in the KNP and surrounding areas (white spots are the masked areas of high tree densities based on the existing land cover).

models. Red edge–based indices were used to estimate leaf N, while leaf area index (LAI) was used to estimate grass biomass. We used empirical regression analysis and both Sentinel-2 and MODIS data to visualize changes in leaf nitrogen between different months (end of the wet season until end of the dry season) and changes in plant biomass among the years 2001, 2006, 2012, and 2015 for the Kruger National Park (South Africa) and surroundings.

Results

Figure 1 and 2 display forage N and biomass maps for the north-eastern part of South Africa, the Kruger National Park and surrounding areas. Red edge–based indices were used to estimate forage N and explained over 75% of leaf N variation. Grass biomass, on the other hand, was estimated using leaf area index (LAI), with the accuracy ranging between 50% and 80% for various dates. The results show clear patterns of grass or forage quality and availability, which are influenced by the underlying geological substrate. Forage quality and availability are also influenced by the frequency of fire (see also Joubert et al., 2018). The maps can be further analysed using any metric required.

Synthesis and outlook

Forage quality and biomass maps could be used as an input for the carrying capacity and stocking rates models for improved rangeland use planning and management. This could ideally reduce land degradation and loss of forage quality. Well-managed grazing areas improve livestock production and food security as well as game habitat utilization and movements, which are important for national parks and game farms. These products could further help in the analysis of how changes in climate influence current and future forage quality and availability (biomass).

B. Impacts on nutritional quality and plant availability

Impact of human land management on plant quality — general introduction

Large herbivores have an enormous impact on terrestrial ecosystems. Under different grazing pressures, vegetation composition and plant biomass might change (e.g., Olff & Ritchie, 1998; Parsons et al., 1994; Peco et al., 2006). Similarly, there could be changes in the chemical composition of plants as a result of feeding damage (e.g., Karban & Myers, 1989; Rooke & Bergström, 2007; Stolter, 2008; Stolter et al., 2005). In anthropogenic grazing systems, where cattle almost entirely substitute wild-ranging herbivores, natural long-distance movements are no longer possible because of the fragmented, often fenced-in landscape. In these areas, overgrazing is a challenge that has detrimental effects on the overall quality of a given habitat, such as by desertification or bush encroachment. Another land management activity that tends to influence the forage quality for both grazers (such as cattle, but also wild herbivores such as common warthog and gemsbok) and browsers (such as greater kudu, giraffe) is the long-held practice of bush burning. This leads to changes in the distribution of animals and consequently to changes in the utilization of an area. Therefore, we investigated the impacts and consequences of overgrazing, browsing, and fire in different projects. The following paragraphs will give extended summaries of these projects (for the influence of fire on plant quality and animal utilization, however, see Joubert et al. [2018] in this book).

Figure 3: Low and wide fences allow wild animals to move between sites.

Fence line and overgrazing

Introduction

Why is it important? Some large herbivores are known for their distinct migratory behaviour influenced by climatic conditions. These migrations often occur along the 'greening line' related to rainfall gradients in Africa or following the snowmelt gradients by large caribou and reindeer herds in Arctic regions. Migration allows herbivores in a seasonally changing environment to fulfil their nutritional needs by feeding on plants of higher quality (Fynn, 2012; Mårell et al., 2006). In addition, it gives already grazed areas time to recover from feeding damage. The naturally occurring migration pattern of some herbivores was adopted by humans during transhumance. With the development of settlements, however, the subdivision of land by fencing resulted in fragmented landscapes, especially when high fences supress every sort of migration and even small-scale movements. Inside the fence, herbivores might overutilize the available plant biomass, leading to changes in plant biodiversity as herbivores select the most palatable plants first (Skarpe, 1990) and changes in soil properties (Gröngröft et al., 2010), with consequences for the associated fauna (e.g., small herbivores, insects, reptiles). In our study (Kesch et al., in print), we determined the differences between areas with high and low grazing pressure using a fence-line contrast.

We determined how standing biomass of grass vegetation and its chemical characteristics differ between sites with low and high grazing pressure (for more details about the methods, see Kesch et al., in print). Furthermore, we determined how much time pasture in heavily grazed areas needs to recover from overgrazing effects.

Methods

Changes in vegetation composition and biomass can be easily seen along fence lines (e.g., along the Khutse Game Reserve in Botswana, where cattle replaced migratory wildlife). Three sampling sites were installed in three different areas, with one intensively grazed by livestock, one that had previously been intensively grazed but that at time of sampling was no longer used by livestock, and one site with low grazing pressure by wildlife. At each site, 21 sampling plots (100 cm²) were installed. Plots were sampled at different times of the year and each plot was cut 5 cm above the ground; samples were pooled for each plot and used for chemical analyses (ADF, NDF, and nitrogen). For a detailed description of the methods, see Kesch et al. (in print).

Results

Interestingly, we found that as a result of the feeding activity of the cattle, the remaining regrowing grass contains higher percentages of protein (high grazing intensity: dry season 6.0 % and wet season 9.9% vs. low grazing intensity: dry season 3.5% and wet season 4.6%) and lower concentrations of ADF and NDF, especially in the wet season (e.g., 35.1% ADF at high grazing intensity vs. 46.1% at the low-grazing-intensity site). Hence, we find a higher general quality of grasses in the heavily grazed region. However, heavy grazing leads to a reduced plant biomass (3 g/100 cm² at high grazing intensity compared to 31 g/100 cm² at low grazing intensity sites measured in the wet season). Furthermore, a shift in vegetation composition was mirrored in a higher abundance of unpalatable plant species (e.g., elephants root, *Elephantorrhiza* spec.). The exclusion of livestock resulted in a rapid increase of grass biomass after one wet season (2 g/100 cm² vs. 15 g/100 cm²), but this was not related to remarkable changes in plant chemical composition (see also Kesch et al., in print).

Synthesis and outlook

The enhanced plant quality (in terms of higher protein concentration) after feeding damage is a phenomenon of plant response reported worldwide in different plant types (grasses: Fanselow et al., 2011; bushes: Stolter et al., 2005; trees: Fornara & Du Toit, 2007). Some grass species in particular are known to be able to compensate for tissue loss (Beaulieu et al., 1996; Hik & Jefferies, 1990), and this compensatory growth is related to higher protein content, as plants need enzymes for regrowth and photosynthesis shortly after damage (but see below for an example of different plant response). Here, we have to point out that plant response is a species-specific reaction to damage and the resulting changes might be very different. But, heavy grazing led to reduced grass biomass in our experiment and in consequence, the absolute amount of protein available per unit area was lower in areas with high than in areas with low grazing pressure. In areas without livestock, the relatively lower quality (in terms of protein content) was compensated by a high availability of biomass. This lower quality range might be suitable for herbivores adapted to lower plant quality (e.g., adapted sheep or herded goats in relatively low numbers). Their feeding damage might lead to a positive feedback loop, depending on the grass species and soil conditions, for subsequent grazers, as described for other herbivores (Hempson et al., 2015).

To prevent overgrazing and subsequent negative impacts such as bush encroachment and desertification in areas where cattle substitutes wild-ranging herbivores, it is necessary to implement rotating grazing systems and adapt stocking rates as well as using a combination of different wild and domestic herbivores for sustainable development (e.g., Dickhoefer et al., 2010; Zimmermann & Smit, 2010). Fences should be adapted to the animals' needs; for example, low and wide fences with an adequate distance to the soil are beneficial for the movement of wild herbivores (Fig. 3) but restrict the movement of cattle.

Bush encroachment: species-specific plant response to damage on seedlings

Introduction

Why is it important? Plants can react to damage in many different ways. These responses can change both plant morphology and plant nutritional quality. In the case of food plants, they might lead to either reutilization (if plant response leads to higher quality; e.g., Stolter, 2008) or avoidance (e.g., if plant response leads to higher concentrations of deterrent substances [PSM] such as phenolics, or mechanical defence such as thorns and spines; e.g., Milewski et al., 1991). In the case of a defensive plant response, damage to bush encroacher species can lead to a higher number of thorns, larger thorns, and higher concentrations of deterrent substances to deter animals from feeding, but also to a lower concentration in nutrients. Therefore, knowledge about plant response is important for developing management strategies for different stakeholders. Especially for bush encroacher species (e.g., different *Acacia* species), this knowledge will aid in understanding and managing the transformation of grassland into thickets of bushes. Furthermore, as some herbivores utilize these plants as a food resource, the animals' feeding choice might offer an opportunity to reduce bush encroacher species, especially if the plants are in the seedling stage. Therefore, we examined how bush encroacher species react to the damage of their top shoot (whether through mechanical cutting by mowing or feeding damage by herbivores) in the seedling stage. We investigated whether damage to top shoots will result in changes in plant chemistry (e.g., lower or higher nitrogen, tannin, or phenolic concentrations) and whether changes in a plant's chemical composition will influence the food choice of sheep or goats. Furthermore, we studied whether sheep or goats prefer to feed on plants with high protein content and avoid plants with high PSM (condensed tannins and total phenolics) concentrations.

Methods

To understand the plant response of important encroacher species, we investigated the plant response of seedlings of *Acacia mellifera* (*Senegalia mellifera*, blackthorn, swarthaak), *A. tortilis* (*Vachellia tortilis*, umbrella thorn acacia), *A. reficiencs* (*Vachellia reficiens*, red bark acacia, rooihak), and *Dichrostachy cinerea* (sicklebush) to top-shoot damage (simulated browsing) in a greenhouse experiment (n = 40 of each species, except *A. tortilis* [n = 20]). Six months after damage, we tested their palatability to sheep and goats (more details about the methods are found in the bush encroachment chapter by Stolter et al. [2018]). For chemical response, we analysed the leaves after simulation of feeding damage for nitrogen, different fibre fractions, condensed tannins, and total phenolics (see Stolter [2018] for more details about the chemistry of feeds). In this chapter we will focus on the chemical response of the plants; results concerning the morphological response and more information about the consequences for subsequent herbivores are also given in the chapter on bush encroachment (Stolter et al., 2018).

Results

Swarthaak (umbrella thorn acacia) had slightly lower concentrations of nitrogen in the leaves of damaged plants compared to control plants; this result was more pronounced for sicklebush (1.77% N in damaged plants vs. 2.23% N in control plants). In this sense, we can see a loss in general quality after damage. Nevertheless, none of the investigated species showed a defensive reaction (which would be reflected in a higher condensed tannins or total phenolic concentration). We detected no remarkable changes in plant chemistry in rooihak.

In a subsequent feeding trial, we tested the influence of the plant response on sheep and goats. Neither sheep nor goats showed differences in selection between previously damaged or undamaged plants (for more detailed information, see the bush encroachment chapter, Stolter et al., 2018). Unlike goats, the chosen sheep breed (Cameroon blackbelly) totally avoided all four plant species, whether the plants were damaged or not. To test whether sheep avoided the plants because of the plants' tannin content, we additionally sprayed the plants with a polyethylene glycol solution (a common method for blocking tannin bioactivity; e.g., Makkar et al., 1995; Silanikove et al., 1994) and offered these plants for another week. However, the sheep still refused to feed on any of the plants offered. Goats, on the other hand, did not discriminate between damaged and control plants and preferred neither the plant species with the highest nitrogen concentration (swarthaak, 3.69% N in leaves of control plants) nor that with the lowest concentration of PSMs (swarthaak has virtually no condensed tannins; 0.63% total phenolics in leaves of control plants). Instead, goats favoured sicklebush, which is lower in nitrogen (2.23% N in leaves of control plants) and higher in PSM concentration (condensed tannins: 1.06%, total phenolics: 1.95% in leaves of control plants) than the other tested bush encroachers (more detailed results will be published by Stolter & Joubert elsewhere).

Synthesis and outlook

In contrast to our expectations, our results show only a slight change in nitrogen, leading to a slightly lower overall plant quality, but no real defensive strategy (e.g., we did not find higher tannins

Figure 4: Open top chambers (OTC) on a bush-cleared site in the thornbush savanna in Namibia (Erichsfelde Farm).

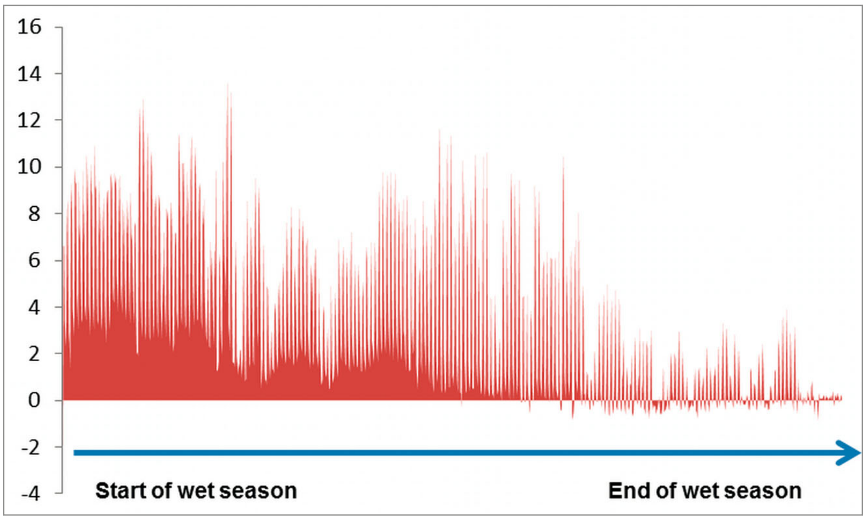

Figure 5: Differences in temperature in °C (y-axis) between inside the OTC and outside (mean of seven chambers per data point, 1,171 data points, measuring interval of 4 hours); time span (x-axis) from October (start of wet season) till May (end of wet season). Note: Differences were less at the end of the rainy season.

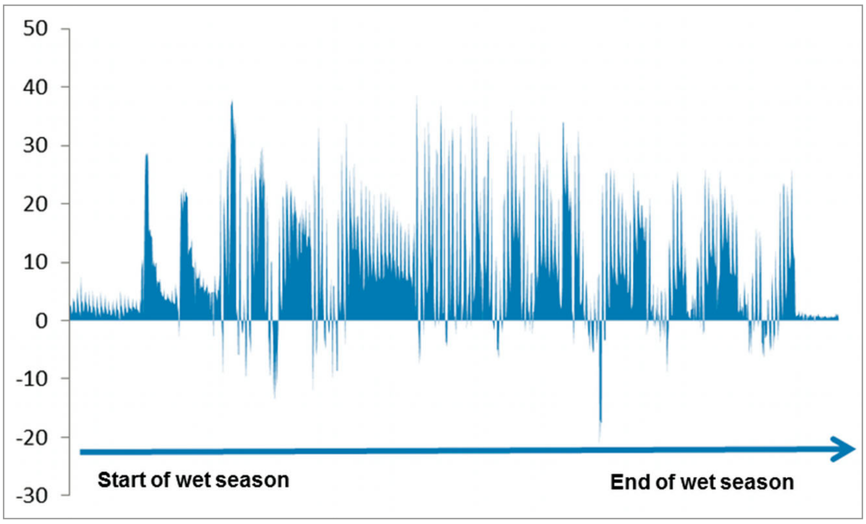

Figure 6: Reduction in relative humidity [%] inside the OTC chamber compared to the outside (y-axis, mean of seven chambers per data point, 1,171 data points, measuring interval of 4 hours); time span (x-axis) from October (start of wet season) till May (end of wet season). Note: There was no seasonally pronounced effect at the end of the rainy season compared to temperature.

content after damage). More interesting was our finding of a severe response in the morphological characteristics of the plants (see bush encroachment chapter, Stolter et al., 2018). Our feeding trial clearly demonstrated that neither do the measured PSMs lead to a total avoidance nor does the high nitrogen content lead to a feeding preference in goats. This result clearly underscores that food selection cannot be simplified to one food component but is rather a product of different trade-offs, as described by the nutrient-balance hypothesis (Felton et al., 2016; Simpson & Raubenheimer, 2012). In our case, food selection seemed to be driven not by plants' chemical content but by their morphological defences. This was related not to the size of the thorns but rather to their shape (Stolter et al., 2018). For management implications, however, the overall high quality of the plants might be interesting, as it is beneficial for herbivores that can cope with the mechanical barrier (e.g., kudu, goats) and the plants can also be used in a ground and pelleted form (to destroy the mechanical defence) as supplementary feeds for cattle. This utilization of these plant species as supplementary food can therefore contribute to the carrying capacity of the savanna ecosystem, especially in times of scarce food availability.

Impact of temperature and rainfall on plant chemical composition — general introduction

As a consequence of climatic changes, we can expect changes in the chemical compositions of plants that might lead to changes in food selection by herbivores. Studies on simulated climate change (e.g., increased temperature, reduced water availability, increased CO_2) lead to ambiguous results concerning changes in plant quality. For example, studies have shown that elevated CO_2 increases the assimilation of carbon. As a result, plant protein concentrations decrease, especially in dicotyledons used as food by browsers (Cotrufo et al., 1998), while concentrations of fibre and C-based PSMs (e.g., phenolics) might increase (Stiling & Cornelissen, 2007, but see Veteli et al., 2002). Furthermore, PSMs are known

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to be more toxic to mammals at higher ambient temperatures and detoxification costs can be enormous (Dearing, 2013; Forbey et al., 2013; Kurnath & Dearing, 2013).

As plant chemical composition is likely to change in response to climate change, the nutritional quality of feed will become a focal point of interest for different stakeholders (researchers, farmers, wildlife managers, nature conservationists, hunters) dealing with the management of large herbivores. To improve our understanding of climate change impacts, we investigated the influence of increased temperature and reduced humidity on the general plant quality of different grass species.

Methods

We installed 32 open-top chambers (OTC) in the thornbush savanna of Namibia (Fig. 4) for a period of seven months.

We used the i-botton data logger to measure differences in temperature and humidity between inside and outside every four hours (Fig. 5 and 6) to ensure that our OTC increased temperature and reduced humidity. For chemical analyses (nitrogen, different fibre fractions, ash), we used five grasses growing naturally in the area: *Pogonarthria fleckii* (annual hairy fishbone grass), *Urochloa brachyura*, *Melis repens* (red top), *Panicum* sp., and *Aristida stipitata* (bristlegrass) from inside and outside (control) the chambers.

Results

The mean difference in temperature between inside and outside the chambers was approximately 2.5°C; additionally, the humidity was reduced (Fig. 5 and 6). We found pronounced differences during the wet season for temperature but not for humidity. We found no significant differences in plant quality for four of our five species. Only bristlegrass showed higher concentrations of different fibre fractions as a result of a higher ADL content in the OTC chamber compared to control (NDF: 76.14% [OTC] vs. 74.68% [control]; ADF: 41.23% [OTC] vs. 39.73% [control]; ADL: 4.29% [OTC] vs. 3.89% [control]). More detailed results will be published by Stolter & Joubert elsewhere.

Synthesis and outlook

Our results indicate that the impact of higher temperature and lower humidity is species-specific. Four of the five tested species showed no difference while bristlegrass showed higher concentration of different fibre fractions mainly because of a higher concentration of ADL (an index of indigestible cell compounds such as lignins). This result indicates a reduction in quality for this species, whereas other grass species seem to be unaffected. More investigation concerning the plant response to changing climatic conditions would be beneficial in adapting management approaches for grassland systems such as by choosing specific adapted grass species for the reseeding of bush-cleared sites.

Conclusion

In this chapter we showed the results of in situ projects and an example of an application of remote sensing to study forage quality and quantity. Both techniques are of high value for developing management systems and enhancing expert knowledge about landscape utilization and management when it comes to large herbivores. Well-managed landscapes are of high importance for future livestock production, game farms, and nature conservation efforts. Knowledge gained from in situ projects (e.g., about changes in plant quality or food selection) are helpful for validating and developing large-scale remote-sensing models, which can improve rangeland planning and management. In this chapter we were able to show that plant responses to different types of damage (cattle grazing, top-shoot damage) and other factors (climate) are species-specific. However, we also demonstrated that food selection is dependent on the herbivore species, making generalizations regarding food quality potentially misleading. Consequently, detailed studies are necessary not only to understand the different impacts on food quality but also to understand the drivers of diet selection. We have a responsibility to transfer this gained knowledge from the laboratory to the field.

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References

Barboza, P.S., Parker, K.L. & Hume, I.D. (2008) *Integrative wildlife nutrition*. Springer Science & Business Media, Berlin.

Beaulieu, J., Gauthier, G. & Rochefort, L. (1996) The growth response of graminoid plants to goose grazing in a High Arctic environment. *Journal of Ecology*, 905–914.

Ben-Shahar, R. & Coe, M.J. (1992) The relationships between soil factors, grass nutrients and the foraging behaviour of wildebeest and zebra. *Oecologia*, **90**, 422–428.

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

Clauss, M., Kaiser, T. & Hummel, J. (2008) The morphophysiological adaptations of browsing and grazing mammals. *The ecology of browsing and grazing*, pp. 47–88. Springer, Berlin.

Cotrufo, M.F., Ineson, P. & Scott, A. (1998) Elevated CO_2 reduces the nitrogen concentration of plant tissues. *Global Change Biology*, **4**, 43–54.

Curran, P.J., Dungan, J.L., Macler, B.A. & Plummer, S.E. (1991) The effect of a red leaf pigment on the relationship between red edge and chlorophyll concentration. *Remote Sensing of Environment*, **35**, 69–76.

Dearing, M.D. (2013) Temperature-dependent toxicity in mammals with implications for herbivores: a review. *Journal of Comparative Physiology B*, **183**, 43–50.

Deutz, A., Gasteiner, J. & Buchgraber, K. (2009) *Fütterung von Reh-und Rotwild: ein Praxisratgeber*. Stocker, Graz.

Dickhoefer, U., Buerkert, A., Brinkmann, K. & Schlecht, E. (2010) The role of pasture management for sustainable livestock production in semi-arid subtropical mountain regions. *Journal of Arid Environments*, **74**, 962–972.

Fanselow, N., Schönbach, P., Gong, X.Y., Lin, S., Taube, F., Loges, R., Pan, Q. & Dittert, K. (2011) Short-term regrowth responses of four steppe grassland species to grazing intensity, water and nitrogen in Inner Mongolia. *Plant and Soil*, **340**, 279–289.

FAO (Food and Agriculture Organization of the United Nations) (2010) Land degradation assessment in drylands (LADA). http://www.fao.org/nr/lada/ (accessed April 2017).

Felton, A.M., Felton, A., Raubenheimer, D., Simpson, S.J., Krizsan, S.J., Hedwall, P.-O. & Stolter, C. (2016) The nutritional balancing act of a large herbivore: an experiment with captive moose (*Alces alces L*). *PLOS One*, **11**, e0150870.

Forbey, J.S., Wiggins, N.L., Frye, G.G. & Connelly, J.W. (2013) Hungry grouse in a warming world: emerging risks from plant chemical defenses and climate change. *Wildlife Biology*, **19**, 374–381.

Fornara, D. & Du Toit, J. (2007) Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African savanna. *Ecology*, **88**, 200–209.

Freeland, W.J. & Janzen, D.H. (1974) Strategies in herbivory by mammals: the role of plant secondary compounds. *The American Naturalist*, **108**, 269–289.

Fynn, R.W. (2012) Functional resource heterogeneity increases livestock and rangeland productivity. *Rangeland Ecology & Management*, **65**, 319–329.

Gröngröft, A., Mager, D., Medinski, T., Mills, A., Petersen, A. & Eschenbach, A. (2010). Evaluation of soil degradation state along fence-line contrasts. *Biodiversity in southern Africa. Vol. 2. Patterns and processes at regional scale*.pp. 207–213. Klaus Hess Publishers, Göttingen & Windhoek.

Harris, A., Carr, A. & Dash, J. (2014) Remote sensing of vegetation cover dynamics and resilience across southern Africa. *International Journal of Applied Earth Observation and Geoinformation*, **28**, 131–139.

Hempson, G.P., Archibald, S., Bond, W.J., Ellis, R.P., Grant, C.C., Kruger, F.J., Kruger, L.M., Moxley, C., Owen-Smith, N. & Peel, M.J. (2015) Ecology of grazing lawns in Africa. *Biological Reviews*, **90**, 979–994.

Hik, D. & Jefferies, R. (1990) Increases in the net above-ground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model. *The Journal of Ecology*, 180–195.

Hofmann, R.R. (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia*, **78**, 443-457.

Hofmann, R.R. (2010) *Wildtiere in Bildern zur vergleichenden Anatomie*. Schlütersche, Hannover.

Iason, G.R. & Villalba, J.J. (2006) Behavioral strategies of mammal herbivores against plant secondary metabolites: the avoidance–tolerance continuum. *Journal of Chemical Ecology*, **32**, 1115–1132.

Joubert, D.F., Stolter, C., Krewenka, K.M., Uunona, N., Amputu, V., Nghalipo, E., Thompson, S., Schütte, K., Kruspe, M., Throop, H., du Preez, P. Beytell, P., le Roux, M. & Aindongo, H. (2018) Impacts of fire history in a semi-arid woodland savanna. This volume.

Karban, R. & Myers, J.H. (1989) Induced plant responses to herbivory. *Annual Review of Ecology and Systematics*, **20**, 331–348.

Kaszta, Ż., Marino, J., Ramoelo, A. & Wolff, E. (2016) Bulk feeder or selective grazer: African buffalo space use patterns based on fine-scale remotely sensed data on forage quality and quantity. *Ecological Modelling*, **323**, 115–122.

Kesch, C., Stolter, C. & Ganzhorn, J.U. (in print). Changes in forage biomass and quality after exclusion of livestock in the southern Kalahari. *Ecotropica*.

Knox, N.M., Skidmore, A.K., Prins, H.H., Heitkönig, I.M., Slotow, R., van der Waal, C. & de Boer, W.F. (2012) Remote sensing of forage nutrients: Combining ecological and spectral absorption feature data. *ISPRS journal of Photogrammetry and Remote Sensing*, **72**, 27–35.

Kurnath, P. & Dearing, M.D. (2013) Warmer ambient temperatures depress liver function in a mammalian herbivore. *Biology Letters*, **9**, 20130562.

Lehmann, C.E.R., Ratnam, J. & Hutley, L. B. (2009) Which of these continents is not like the other? Comparisons of tropical savanna systems: key questions and challenges. *New Phytologist*, **181**, 508–511.

Mao, S., Zhang, R., Wang, D. & Zhu, W. (2013) Impact of subacute ruminal acidosis (SARA) adaptation on rumen microbiota in dairy cattle using pyrosequencing. *Anaerobe*, **24**, 12–19.

Makkar, H.P.S., Blümmel, M. & Becker, K. (1995). Formation of complexes between polyvinyl pyrrolidones or polyethylene glycols and tannins, and their implication in gas production and true digestibility in in vitro techniques. *British Journal of Nutrition*, **73**, 897–913.

Mårell, A., Hofgaard, A. & Danell, K. (2006) Nutrient dynamics of reindeer forage species along snowmelt gradients at different ecological scales. *Basic and Applied Ecology*, **7**, 13–30.

Milewski, A.V., Young, T.P. & Madden, D. (1991) Thorns as induced defenses: experimental evidence. *Oecologia*, **86**, 70–75.

Murphy, B.P., Andersen, A.N. & Parr, C.L. (2016) The underestimated biodiversity of tropical grassy biomes. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **371**, 20150319.

Mutanga, O. & Skidmore, A. (2004) Integrating imaging spectroscopy and neural networks to map grass quality in the Kruger National Park, South Africa. *Remote Sensing of Environment*, **90**, 104–115.

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

Olff, H. & Ritchie, M.E. (1998) Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution*, **13**, 261–265.

Palmer, A.R. & Bennett, J.E. (2013) Degradation of communal rangelands in South Africa: towards an improved understanding to inform policy. *African Journal of Range & Forage Science*, **30**, 57–63.

Parsons, A., Newman, J., Penning, P., Harvey, A. & Orr, R. (1994) Diet preference of sheep: effects of recent diet, physiological state and species abundance. *Journal of Animal Ecology*, 465–478.

Peco, B., Sánchez, A.M. & Azcárate, F.M. (2006) Abandonment in grazing systems: consequences for vegetation and soil. *Agriculture, Ecosystems & Environment*, **113**, 284–294.

Petri, R.M., Schwaiger, T., Penner, G.B., Beauchemin, K.A., Forster, R.J., McKinnon, J.J. & McAllister, T.A. (2013) Characterization of the core rumen microbiome in cattle during transition from forage to concentrate as well as during and after an acidotic challenge. *PLOS One*, **8**, e83424.

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

Ramoelo, A. & Cho, M. A. (2018) Explaining leaf nitrogen distribution in a semi-arid environment predicted on Sentinel-2 imagery using a field spectroscopy derived model. *Remote Sensing*, **10**, 269.

Ramoelo, A., Cho, M.A., Mathieu, R., Madonsela, S., Van De Kerchove, R., Kaszta, Z. & Wolff, E. (2015a) Monitoring grass nutrients and biomass as indicators of rangeland quality and quantity using random forest modelling and WorldView-2 data. *International Journal of Applied Earth Observation and Geoinformation*, **43**, 43–54.

Ramoelo, A., Cho, M., Mathieu, R. & Skidmore, A.K. (2015b) Potential of Sentinel-2 spectral configuration to assess rangeland quality. *Journal of Applied Remote Sensing*, **9**, 094096–094096.

Ramoelo, A., Skidmore, A., Cho, M.A., Mathieu, R., Heitkönig, I., Dudeni-Tlhone, N., Schlerf, M. & Prins, H. (2013) Non-linear partial least square regression increases the estimation accuracy of grass nitrogen and phosphorus using in situ hyperspectral and environmental data. *ISPRS Journal of Photogrammetry and Remote Sensing*, **82**, 27–40.

Ramoelo, A., Skidmore, A.K., Cho, M.A., Schlerf, M., Mathieu, R. & Heitkönig, I.M. (2012) Regional estimation of savanna grass nitrogen using the red-edge band of the spaceborne RapidEye sensor. *International Journal of Applied Earth Observation and Geoinformation*, **19**, 151–162.

Ramoelo, A., Stolter, C., Joubert, D.F., Cho, M.A., Groengroeft, A., Madibela, O.R., Zimmermann, I. & Pringle, H. (2018) Rangeland monitoring and assessment: overview. This volume.

Robbins, C., Hanley, T., Hagerman, A., Hjeljord, O., Baker, D., Schwartz, C. & Mautz, W. (1987) Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology*, **68**, 98–107.

Rooke, T. & Bergström, R. (2007) Growth, chemical responses and herbivory after simulated leaf browsing in *Combretum apiculatum*. *Plant Ecology*, **189**, 201–212.

Simpson, S.J. & Raubenheimer, D. (2012) *The nature of nutrition: a unifying framework from animal adaptation to human obesity*. Princeton University Press, Princeton, NJ, USA.

Silanikove, N., Nitsan, Z. & Perevolotsky, A. (1994) Effect of a daily supplementation of poly (ethylene glycol) on intake and digestion of tannin-containing leaves (*Ceratonia siliqua*) by sheep. *Journal of Agricultural and Food Chemistry*, **42**, 2844–2847.

Skarpe, C. (1990) Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. *Journal of Applied Ecology*, 873–885.

Skidmore, A.K., Ferwerda, J. G., Mutanga, O., Van Wieren, S.E., Peel, M., Grant, R.C., Prins, H.H., Balcik, F.B. & Venus, V. (2010) Forage quality of savannas – Simultaneously mapping foliar protein and polyphenols for trees and grass using hyperspectral imagery. *Remote Sensing of Environment*, **114**, 64–72.

Stevens, C.E. & Hume, I.D. (1998) Contributions of microbes in vertebrate gastrointestinal tract to production and conservation of nutrients. *Physiological Reviews*, **78**, 393–427.

Stiling, P. & Cornelissen, T. (2007) How does elevated carbon dioxide (CO2) affect plant–herbivore interactions? A field experiment and meta-analysis of CO2-mediated changes on plant chemistry and herbivore performance. *Global Change Biology*, **13**, 1823–1842.

Stolter, C. (2008) Intra-individual plant response to moose browsing: feedback loops and impacts on mulitple consumers. *Ecological Monographs*, **78**, 167–183.

Stolter, C. (2018) What is quality for a ruminant? A short introduction to the meaning of plant chemical composition measurements. This volume.

Stolter, C., Ball, J.P., Julkunen-Tiitto, R., Lieberei, R. & Ganzhorn, J.U. (2005) Winter browsing of moose on two different willow species: food selection in relation to plant chemistry and plant response. *Canadian Journal of Zoology*, **83**, 807–819.

Stolter, C., Joubert, D.F., Schwarz, K. & Finckh, M. (2018) Two different issues of bush encroachment management: plant response and animal distribution. This volume.

Thornton, P.K. (2010) Livestock production: recent trends, future prospects. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **365**, 2853–2867.

Van Soest, P.J. (1994) *Nutritional ecology of the ruminant*. Cornell University Press, Ithaca, NY, USA.

Veteli, T., Kuokkanen, K., Julkunen-Tiitto, R., Roininen, H. & Tahvanainen, J. (2002) Effects of elevated CO_2 and temperature on plant growth and herbivore defensive chemistry. *Global Change Biology*, **8**, 1240–1252.

Villalba, J.J., Provenza, F.D. & Bryant, J. (2002) Consequences of the interaction between nutrients and plant secondary metabolites on herbivore selectivity: benefits or detriments for plants? *Oikos*, **97**, 282–292.

Westoby, M. (1974) An analysis of diet selection by large generalist herbivores. *The American Naturalist*, **108**, 290–304.

Zimmermann, I. & Smit, G.N. (2010) Impact of landuse at landscape scale, using fenceline contrasts and a best-practice case study. *Biodiversity in Southern Africa. Vol. 2. Patterns and processes at regional scale.* pp.214–221. Klaus Hess Publishers, Göttingen & Windhoek.

References [CrossRef]

Barboza, P.S., Parker, K.L. & Hume, I.D. (2008) *Integrative wildlife nutrition*. Springer Science & Business Media, Berlin.

Beaulieu, J., Gauthier, G. & Rochefort, L. (1996) The growth response of graminoid plants to goose grazing in a High Arctic environment. *Journal of Ecology*, 905–914. CrossRef

Ben-Shahar, R. & Coe, M.J. (1992) The relationships between soil factors, grass nutrients and the foraging behaviour of wildebeest and zebra. *Oecologia*, **90**, 422–428. CrossRef

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

Clauss, M., Kaiser, T. & Hummel, J. (2008) The morphophysiological adaptations of browsing and grazing mammals. *The ecology of browsing and grazing*, pp. 47–88. Springer, Berlin. CrossRef

Cotrufo, M.F., Ineson, P. & Scott, A. (1998) Elevated CO2 reduces the nitrogen concentration of plant tissues. *Global Change Biology*, **4**, 43–54. CrossRef

Curran, P.J., Dungan, J.L., Macler, B.A. & Plummer, S.E. (1991) The effect of a red leaf pigment on the relationship between red edge and chlorophyll concentration. *Remote Sensing of Environment*, **35**, 69–76. CrossRef

Dearing, M.D. (2013) Temperature-dependent toxicity in mammals with implications for herbivores: a review. *Journal of Comparative Physiology B*, **183**, 43–50. CrossRef

Deutz, A., Gasteiner, J. & Buchgraber, K. (2009) *Fütterung von Reh-und Rotwild: ein Praxisratgeber*. Stocker, Graz.

Dickhoefer, U., Buerkert, A., Brinkmann, K. & Schlecht, E. (2010) The role of pasture management for sustainable livestock production in semi-arid subtropical mountain regions. *Journal of Arid Environments*, **74**, 962–972. CrossRef

Fanselow, N., Schönbach, P., Gong, X.Y., Lin, S., Taube, F., Loges, R., Pan, Q. & Dittert, K. (2011) Short-term regrowth responses of four steppe grassland species to grazing intensity, water and nitrogen in Inner Mongolia. *Plant and Soil*, **340**, 279–289. CrossRef

FAO (Food and Agriculture Organization of the United Nations) (2010) Land degradation assessment in drylands (LADA). http://www.fao.org/nr/lada/ (accessed April 2017).

Felton, A.M., Felton, A., Raubenheimer, D., Simpson, S.J., Krizsan, S.J., Hedwall, P.-O. & Stolter, C. (2016) The nutritional balancing act of a large herbivore: an experiment with captive moose (*Alces alces L*). *PLOS One*, **11**, e0150870. CrossRef

Forbey, J.S., Wiggins, N.L., Frye, G.G. & Connelly, J.W. (2013) Hungry grouse in a warming world: emerging risks from plant chemical defenses and climate change. *Wildlife Biology*, **19**, 374–381. CrossRef

Fornara, D. & Du Toit, J. (2007) Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African savanna. *Ecology*, **88**, 200–209. CrossRef

Freeland, W.J. & Janzen, D.H. (1974) Strategies in herbivory by mammals: the role of plant secondary compounds. *The American Naturalist*, **108**, 269–289. CrossRef

Fynn, R.W. (2012) Functional resource heterogeneity increases livestock and rangeland productivity. *Rangeland Ecology & Management*, **65**, 319–329. CrossRef

Gröngröft, A., Mager, D., Medinski, T., Mills, A., Petersen, A. & Eschenbach, A. (2010). Evaluation of soil degradation state along fence-line contrasts. *Biodiversity in southern Africa. Vol. 2. Patterns and processes at regional scale*.pp. 207–213. Klauss Hess Publishers, Göttingen & Windhoek.

Harris, A., Carr, A. & Dash, J. (2014) Remote sensing of vegetation cover dynamics and resilience across southern Africa. *International Journal of Applied Earth Observation and Geoinformation*, **28**, 131–139. CrossRef

Hempson, G.P., Archibald, S., Bond, W.J., Ellis, R.P., Grant, C.C., Kruger, F.J., Kruger, L.M., Moxley, C., Owen-Smith, N. & Peel, M.J. (2015) Ecology of grazing lawns in Africa. *Biological Reviews*, **90**, 979–994. CrossRef

Hik, D. & Jefferies, R. (1990) Increases in the net above-ground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model. *The Journal of Ecology*, 180–195. CrossRef

Hofmann, R.R. (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia*, **78**, 443-457. CrossRef

Hofmann, R.R. (2010) *Wildtiere in Bildern zur vergleichenden Anatomie*. Schlütersche, Hannover.

Iason, G.R. & Villalba, J.J. (2006) Behavioral strategies of mammal herbivores against plant secondary metabolites: the avoidance–tolerance continuum. *Journal of Chemical Ecology*, **32**, 1115–1132. CrossRef

Joubert, D.F., Stolter, C., Krewenka, K.M., Uunona, N., Amputu, V., Nghalipo, E., Thompson, S., Schütte, K., Kruspe, M., Throop, H., du Preez, P. Beytell, P., le Roux, M. & Aindongo, H. (2018) Impacts of fire history in a semi-arid woodland savanna. This volume. CrossRef

Karban, R. & Myers, J.H. (1989) Induced plant responses to herbivory. *Annual Review of Ecology and Systematics*, **20**, 331–348. CrossRef

Kaszta, Ż., Marino, J., Ramoelo, A. & Wolff, E. (2016) Bulk feeder or selective grazer: African buffalo space use patterns based on fine-scale remotely sensed data on forage quality and quantity. *Ecological Modelling*, **323**, 115–122. CrossRef

Kesch, C., Stolter, C. & Ganzhorn, J.U. (in print). Changes in forage biomass and quality after exclusion of livestock in the southern Kalahari. *Ecotropica*.

Knox, N.M., Skidmore, A.K., Prins, H.H., Heitkönig, I.M., Slotow, R., van der Waal, C. & de Boer, W.F. (2012) Remote sensing of forage nutrients: Combining ecological and spectral absorption feature data. *ISPRS journal of Photogrammetry and Remote Sensing*, **72**, 27–35. CrossRef

Kurnath, P. & Dearing, M.D. (2013) Warmer ambient temperatures depress liver function in a mammalian herbivore. *Biology Letters*, **9**, 20130562. CrossRef

Lehmann, C.E.R., Ratnam, J. & Hutley, L. B. (2009) Which of these continents is not like the other? Comparisons of tropical savanna systems: key questions and challenges. *New Phytologist*, **181**, 508–511. CrossRef

Mao, S., Zhang, R., Wang, D. & Zhu, W. (2013) Impact of subacute ruminal acidosis (SARA) adaptation on rumen microbiota in dairy cattle using pyrosequencing. *Anaerobe*, **24**, 12–19. CrossRef

Makkar, H.P.S., Blümmel, M. & Becker, K. (1995). Formation of complexes between polyvinyl pyrrolidones or polyethylene glycols and tannins, and their implication in gas production and true digestibility in in vitro techniques. *British Journal of Nutrition*, **73**, 897–913. CrossRef

Mårell, A., Hofgaard, A. & Danell, K. (2006) Nutrient dynamics of reindeer forage species along snowmelt gradients at different ecological scales. *Basic and Applied Ecology*, **7**, 13–30. CrossRef

Milewski, A.V., Young, T.P. & Madden, D. (1991) Thorns as induced defenses: experimental evidence. *Oecologia*, **86**, 70–75. CrossRef

Murphy, B.P., Andersen, A.N. & Parr, C.L. (2016) The underestimated biodiversity of tropical grassy biomes. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **371**, 20150319. CrossRef

Mutanga, O. & Skidmore, A. (2004) Integrating imaging spectroscopy and neural networks to map grass quality in the Kruger National Park, South Africa. *Remote Sensing of Environment*, **90**, 104–115. CrossRef

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

Olff, H. & Ritchie, M.E. (1998) Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution*, **13**, 261–265. CrossRef

Palmer, A.R. & Bennett, J.E. (2013) Degradation of communal rangelands in South Africa: towards an improved understanding to inform policy. *African Journal of Range & Forage Science*, **30**, 57–63. CrossRef

Parsons, A., Newman, J., Penning, P., Harvey, A. & Orr, R. (1994) Diet preference of sheep: effects of recent diet, physiological state and species abundance. *Journal of Animal Ecology*, 465–478. CrossRef

Peco, B., Sánchez, A.M. & Azcárate, F.M. (2006) Abandonment in grazing systems: consequences for vegetation and soil. *Agriculture, Ecosystems & Environment*, **113**, 284–294. CrossRef

Petri, R.M., Schwaiger, T., Penner, G.B., Beauchemin, K.A., Forster, R.J., McKinnon, J.J. & McAllister, T.A. (2013) Characterization of the core rumen microbiome in cattle during transition from forage to concentrate as well as during and after an acidotic challenge. *PLOS One*, **8**, e83424. CrossRef

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

Ramoelo, A. & Cho, M. A. (2018) Explaining leaf nitrogen distribution in a semi-arid environment predicted on Sentinel-2 imagery using a field spectroscopy derived model. *Remote Sensing*, **10**, 269. CrossRef

Ramoelo, A., Cho, M.A., Mathieu, R., Madonsela, S., Van De Kerchove, R., Kaszta, Z. & Wolff, E. (2015a) Monitoring grass nutrients and biomass as indicators of rangeland quality and quantity using random forest modelling and WorldView-2 data. *International Journal of Applied Earth Observation and Geoinformation*, **43**, 43–54. CrossRef

Ramoelo, A., Cho, M., Mathieu, R. & Skidmore, A.K. (2015b) Potential of Sentinel-2 spectral configuration to assess rangeland quality. *Journal of Applied Remote Sensing*, **9**, 094096–094096. CrossRef

Ramoelo, A., Skidmore, A., Cho, M.A., Mathieu, R., Heitkönig, I., Dudeni-Tlhone, N., Schlerf, M. & Prins, H. (2013) Non-linear partial least square regression increases the estimation accuracy of grass nitrogen and phosphorus using in situ hyperspectral and environmental data. *ISPRS Journal of Photogrammetry and Remote Sensing*, **82**, 27–40. CrossRef

Ramoelo, A., Skidmore, A.K., Cho, M.A., Schlerf, M., Mathieu, R. & Heitkönig, I.M. (2012) Regional estimation of savanna grass nitrogen using the red-edge band of the spaceborne RapidEye sensor. *International Journal of Applied Earth Observation and Geoinformation*, **19**, 151–162. CrossRef

Ramoelo, A., Stolter, C., Joubert, D.F., Cho, M.A., Groengroeft, A., Madibela, O.R., Zimmermann, I. & Pringle, H. (2018) Rangeland monitoring and assessment: overview. This volume. CrossRef

Robbins, C., Hanley, T., Hagerman, A., Hjeljord, O., Baker, D., Schwartz, C. & Mautz, W. (1987) Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology*, **68**, 98–107. CrossRef

Rooke, T. & Bergström, R. (2007) Growth, chemical responses and herbivory after simulated leaf browsing in *Combretum apiculatum*. *Plant Ecology*, **189**, 201–212. CrossRef

Simpson, S.J. & Raubenheimer, D. (2012) *The nature of nutrition: a unifying framework from animal adaptation to human obesity*. Princeton University Press, Princeton, NJ, USA. CrossRef

Silanikove, N., Nitsan, Z. & Perevolotsky, A. (1994) Effect of a daily supplementation of poly (ethylene glycol) on intake and digestion of tannin-containing leaves (*Ceratonia siliqua*) by sheep. *Journal of Agricultural and Food Chemistry*, **42**, 2844–2847. CrossRef

Skarpe, C. (1990) Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. *Journal of Applied Ecology*, 873–885. CrossRef

Skidmore, A.K., Ferwerda, J. G., Mutanga, O., Van Wieren, S.E., Peel, M., Grant, R.C., Prins, H.H., Balcik, F.B. & Venus, V. (2010) Forage quality of savannas — Simultaneously mapping foliar protein and polyphenols for trees and grass using hyperspectral imagery. *Remote Sensing of Environment*, **114**, 64–72. CrossRef

Stevens, C.E. & Hume, I.D. (1998) Contributions of microbes in vertebrate gastrointestinal tract to production and conservation of nutrients. *Physiological Reviews*, **78**, 393–427. CrossRef

Stiling, P. & Cornelissen, T. (2007) How does elevated carbon dioxide (CO2) affect plant–herbivore interactions? A field experiment and meta-analysis of CO2-mediated changes on plant chemistry and herbivore performance. *Global Change Biology*, **13**, 1823–1842. CrossRef

Stolter, C. (2008) Intra-individual plant response to moose browsing: feedback loops and impacts on mulitple consumers. *Ecological Monographs*, **78**, 167–183. CrossRef

Stolter, C. (2018) What is quality for a ruminant? A short introduction to the meaning of plant chemical composition measurements. This volume. CrossRef

Stolter, C., Ball, J.P., Julkunen-Tiitto, R., Lieberei, R. & Ganzhorn, J.U. (2005) Winter browsing of moose on two different willow species: food selection in relation to plant chemistry and plant response. *Canadian Journal of Zoology*, **83**, 807–819. CrossRef

Stolter, C., Joubert, D.F., Schwarz, K. & Finckh, M. (2018) Two different issues of bush encroachment management: plant response and animal distribution. This volume. CrossRef

Thornton, P.K. (2010) Livestock production: recent trends, future prospects. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **365**, 2853–2867. CrossRef

Van Soest, P.J. (1994) *Nutritional ecology of the ruminant*. Cornell University Press, Ithaca, NY, USA.

Veteli, T., Kuokkanen, K., Julkunen-Tiitto, R., Roininen, H. & Tahvanainen, J. (2002) Effects of elevated CO_2 and temperature on plant growth and herbivore defensive chemistry. *Global Change Biology*, **8**, 1240–1252. CrossRef

Villalba, J.J., Provenza, F.D. & Bryant, J. (2002) Consequences of the interaction between nutrients and plant secondary metabolites on herbivore selectivity: benefits or detriments for plants? *Oikos*, **97**, 282–292. CrossRef

Westoby, M. (1974) An analysis of diet selection by large generalist herbivores. *The American Naturalist*, **108**, 290–304. CrossRef

Zimmermann, I. & Smit, G.N. (2010) Impact of landuse at landscape scale, using fenceline contrasts and a best-practice case study. *Biodiversity in Southern Africa. Vol. 2. Patterns and processes at regional scale.* pp.214–221. Klauss Hess Publishers, Göttingen & Windhoek.