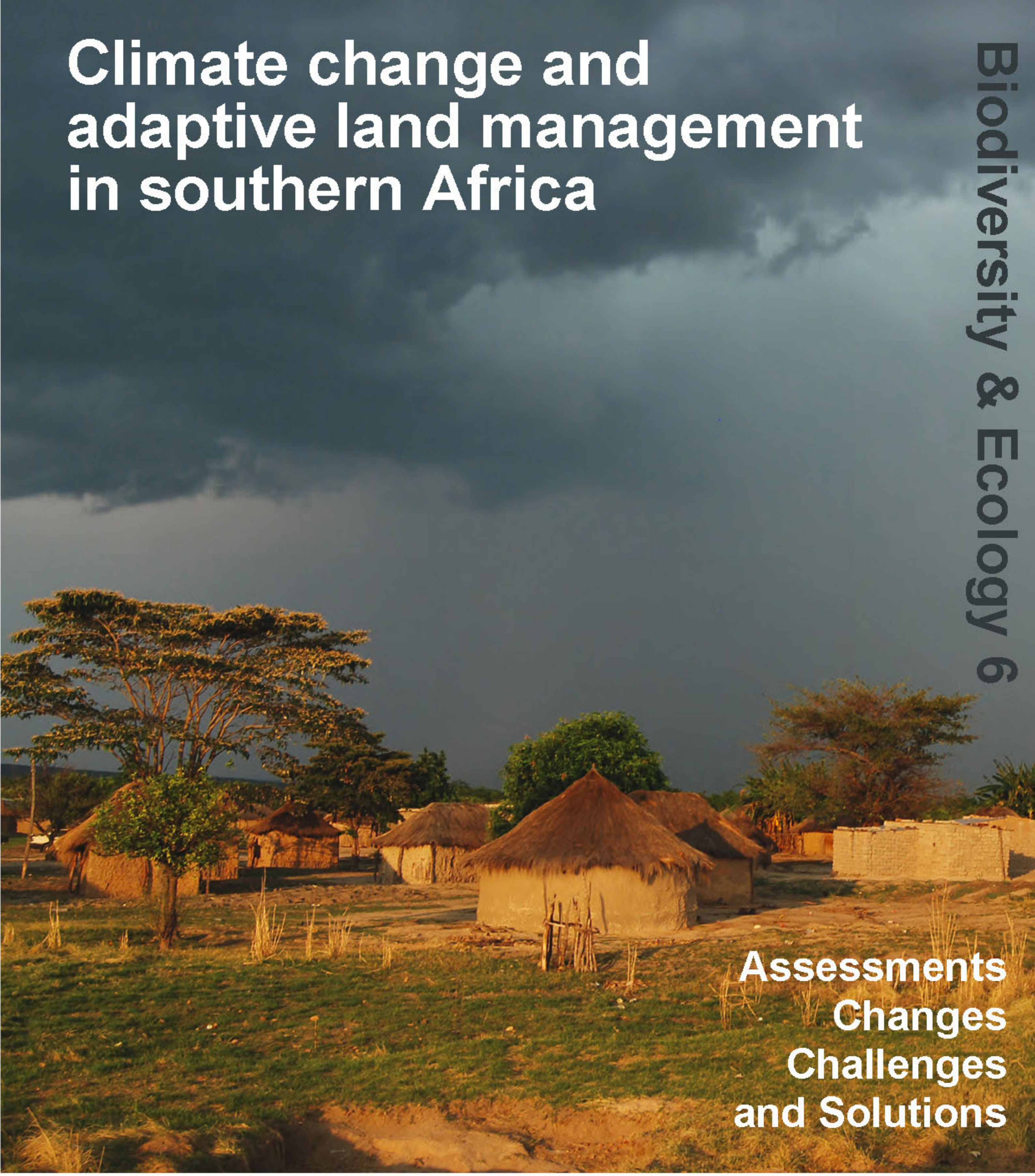
Climate change and adaptive land management in southern Africa

Biodiversity & Ecology 6



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What is quality for a ruminant? A short introduction to the meaning of plant chemical composition measurements

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Rangelands

The "quality" of a given food item depends on the morphological adaptations and physiological requirements of the animal (Stolter et al., 2018). For ruminants the digestion of feeds by the microbiome is essential, therefore food selection is an indirect process. As a result, determining of the drivers behind food selection (e.g. plant quality) is a challenging issue. Nevertheless, some general assumptions about quality can be made:

Energy

It has often been assumed that animals should select for energy-rich food to gain the most benefit of a selected food item in combination with the lowest costs for searching. Energy can be derived from different nutrients. Even though fat gives the most energy, for herbivores energy originates mainly from fibre (mainly cellulose and hemicellulose, see van Soest, 1994), as plants are rich in fibre but low in fat and protein content; energy is gained in an indirect way. In the case of ruminants, most energy is delivered as small chain fatty acids produced by the symbionts of the microbiome in the rumen fermenting different fibre fractions. Therefore, the most common species of this microbiome represent primary degraders (e.g., of cellulose, hemicellulose; Wallace, 2008) due to the natural food of herbivores. This way of digestion is a special adaptation for feeding on plants and is different to that of other animals (such as carnivores or omnivores). This type of feeding must therefore be taken into account when we think of "high quality" food for a ruminant. For example, protein- or carbohydrate-rich feeds are generally expected to be of high nutritional value. Caution must be taken, however, in giving "easily digestible" feeds that contain high concentrations of soluble carbohydrates such as starch (e.g., in grain and corn), low-molecular-weight carbohydrates (e.g., sugar rich fruits), and high amounts of protein to ruminants that are not able to balance the over-ingestion of unfamiliar food (e.g., ruminants in captivity or animal fed with supplementary feeds in the wild). These highly unbalanced diets can lead to detrimental effects on the microbiome such as rumen acidosis or alkalosis (Deutz et al., 2009; Mao et al., 2013) with strong negative effects on animals ranging from diarrhoea to sudden death (sepsis, resulting from excessive loss of rumen symbionts).

Energy is often measured as total or gross energy (e.g., by using calorimetric bombs. It is important to note, however, that these measurements do not distinguish between digestible and indigestible compounds (e.g., indigestible wood will give nearly the same energy content as digestible leaves).

Fibre and other carbohydrates

Fibre is a term that describes the structural carbohydrates of plant cells, which are mainly hemicellulose and cellulose. Lignin, which belongs chemically to the phenolics (a group of plant secondary metabolites), is normally included in this group of compounds. Even though soluble carbohydrates (e.g., sugar, starch) are much easier to digest, ruminants have adapted to digest hemicellulose and cellulose. As mentioned above, feeding high concentrations of soluble carbohydrates can lead to fatal consequences for ruminants, in contrast, the end products (small-chain fatty acids) of the fermentation of hemicellulose and cellulose provide up to 80% of the required energy for the animal (Barboza et al., 2008), while lignin is almost indigestible (Van Soest, 1994). Often food with "high fibre" concentration is assumed to be of "low quality" mainly because of long retention times in the digestive system. As part of the adaptation of ruminants to fibrous feeds, however, the retention time in the rumen is supposed to be long, because rumen symbionts simply need time for fermentation. Differences in the concentrations of fibre fractions in different food plants (e.g. grasses

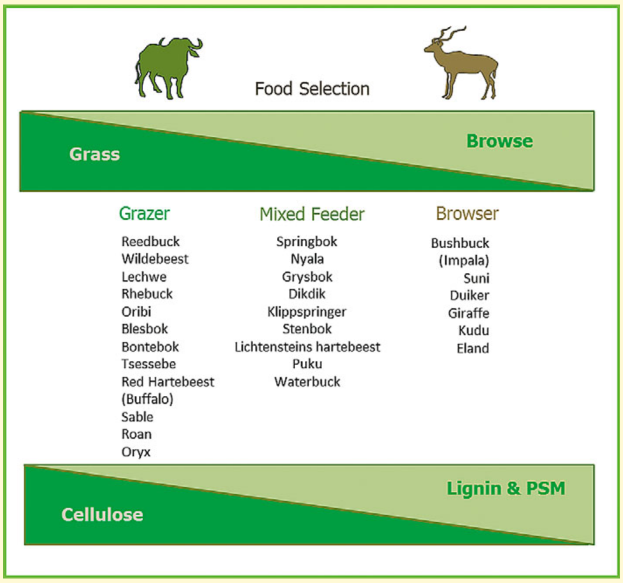

Figure 1. Examples of different feeding types of ruminants, their food selection, and the amount of cellulose, PSM and lignin in their diets, which is related to their tolerance and / or ability to ingest and digest these food items. Note, that grazers do not live exclusively on grasses, nor do browsers feed exclusively on browse.

Rangelands

vs. browse) have led to diverse morphological and physiological adaptations in ruminants resulting in different feeding types (Fig 1). Furthermore, the microbiome of ruminants confronted with different fibre concentrations during different seasons, will react by changing the composition and function of the symbiontic community (Sundset et al., 2009).

Similar to energy, "fibre" is a mixture of different compounds and therefore different fibre fractions can be analysed, e.g. the detergent fibre analysis, Van Soest analysis. Here the plant cell material is divided into soluble cell and cell wall constituents (NDF, ADF and ADL are given; see Fig. 2 for further explanations).

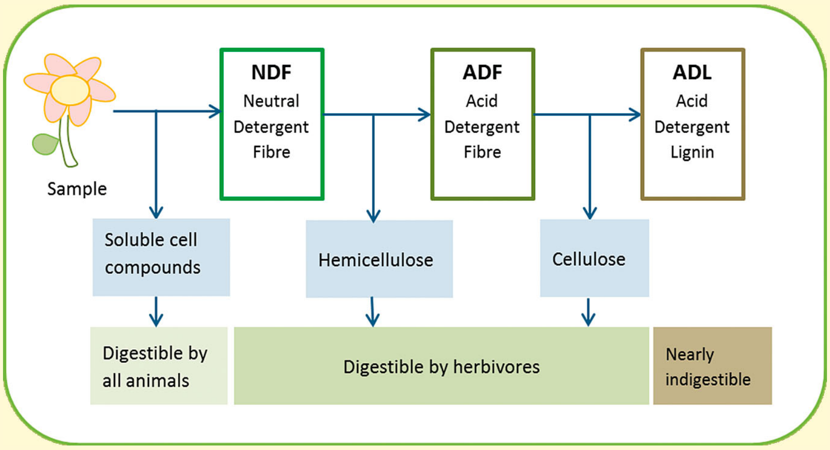

Figure 2. Explanation of the van Soest analyses for fibre. During these analyses different plant constituents are washed out (soluble cell compounds, hemicellulose, cellulose) while NDF, ADF, and ADL remain. A high NDF value can indicate either easily digestible soluble compounds, digestible cellulose and hemicellulose or a high concentration of indigestible lignin. As a consequence, assumptions about "general quality" can be gained only by comparing each fraction or by calculating the differences between NDF, ADF and ADL.

Protein

Protein, often indexed by the nitrogen concentration in the food, is indeed an important nutrient. The general low level of protein in plants, compared to meat, has led to the assumption that herbivores are limited in protein and therefore should maximize their protein intake (e.g. protein maximization hypothesis, see Mattson, 1980) and consequently select plants with high protein concentrations. However, ruminants have evolved physiological adaptations to overcome this problem. Instead of excreting large amounts of nitrogen via urea, ruminants have a recycling system that enables them to transfer metabolic nitrogen back into the rumen, where the microbial symbionts are able to use this nitrogen to build body´s own microbial amino acids which are the basic elements of protein. After their lifetime the microbes are frequently washed from the rumen into lower parts of the gastrointestinal tract, where they are digested and the amino acids of the protein are absorbed (Barboza et al., 2008). This process might be beneficial as non-organic nitrogen from urea is already transferred into amino acids by the rumen microbes. The amino acids can be used by the ruminant to form body´s own protein, instead of building amino acids by themselves in the first step (see also Madibela et al., 2018).

Minerals – The importance of other sources

Minerals are very important for the health of herbivores, e.g. for the development of their skeleton and for muscle contractions, nerve tissue metabolism, and immune response (Barboza et al., 2008; Robbins, 2012). The ingestion of minerals (e.g. Ca, P, Na, Cl, K, Mg, S, Co, Cu, I, Fe, Mn, Se, Zn) is essential, as animals are not able to produce minerals by themselves. Plants are not especially mineral rich and the concentration and composition of a certain food plant does not match the requirements of the foraging animals. Therefore, herbivores often use non-food resources to satisfy their needs. This use has been observed for many mammals, e.g. geophagy by elephants and primates and visits to human latrines by two-toed sloths (Krishnamani & Mahaney, 2000; Holdø et al., 2002; Heymann et al., 2011).

Plant secondary metabolites (PSMs)

PSMs have been assumed to have negative effects on diet selection of mammals due to their toxicity or deterrent effects (Freeland & Janzen, 1974; Bryant & Kuropat, 1980). However, the composition of specific compounds and their effects are not well understood. Our understanding is still hampered by the mostly unknown chemical structures and the lack of analyses to measure the bioactivity of these compounds (see also Rautio et al., 2007; Salminen & Karonen, 2011).

The effects on the animal are largely depending on the dose (Villalba et al. 2002), on the type of compound ingested, on other ingested food compounds and on the adaptation of the herbivore. There is an increasing tolerance to PSMs in general along the gradient from grazers to browsers (Iason & Villalba, 2006, see Fig 1.). In principal, the physiological effects of PSMs can be distinguished by their mode of action, e.g., deterrence by smell or taste, inhibitory effects of digestion or high toxicity (e.g. Hagerman et al., 1992; Stolter et al., 2005; Edlich & Stolter, 2012). The latter might have the highest priority as drivers of diet selection. But in contrast to some domestic animals, wild ruminants can often discriminate toxic plants. Detoxification of specific PSM is often related to a specific pathway. If diets of generalist herbivores are restricted to single species this detoxification pathway might be blocked by ingesting high amounts of a certain PSM (Freeland & Janzen, 1974; Marsh et al., 2006). Consequently, especially for generalists it can be advantageous to consume a multi-species diet (Foley & Moore, 2005). If animals have to live on a restricted diet (e.g. during dry seasons or winter), the only possibility to overcome this bottleneck might be selectivity for low concentrations of PSM as avoidance is simply not possible (Stolter et al., 2013). However, PSMs do not only appear to have negative effects on the consuming animal, but beneficial effects of their ingestion have also been identified.

In particular tannins are known to interact with nutrients such as protein und carbohydrates by building complexes assumed to reduce the quality of the ingested food (e.g. Makkar et al., 1988; Lorenz et al., 2014; but see Salminen & Karonen, 2011). On the other hand, animals on restricted or inappropriate, unbalanced diets (e.g. supplementary feeding, captivity, or livestock) will profit from this complex binding capacity of tannins, e.g. by binding over-ingested carbohydrates or protein. Furthermore, tannins can have various positive effects on ruminants, such as the reduction of internal parasites, increasing milk production, and the reduction of the risk of bloat (Min et al., 2003; Lyman et al., 2008). These contradictions between positive and negative effects might be explained by the differences in chemical structure as the term "tannins" describes a large group of different substances and every plant species has its own composition. More information about tannins is given in Madibela et al. (2018).

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