



# Climate and vegetation in a semi-arid savanna: Development of a climate–vegetation response model linking plant metabolic performance to climate and the effects on forage availability for large herbivores

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A framework to establish the expected effects of climate on forage quantity and quality in a local savanna system was developed to interpret large herbivore population performance patterns in the Kruger National Park. We developed a climate–vegetation response model based on interpretation and synthesis of existing knowledge (literature review) and supported by investigation and analyses of local patterns of climate effects on forage plant performance and chemical composition.

Developing the climate–vegetation response model involved three main components, namely (1) defining indicators of forage availability to herbivores (nitrogen productivity, nitrogen quality, carbon-nutrient quality), (2) identifying herbivore species guilds of similar nutritional requirements with respect to these indicators [bulk feeders with tolerance to fibrous herbage (buffalo, waterbuck), bulk feeders with preference for high nitrogen quality forage (short grass preference grazers: blue wildebeest and zebra) and selective feeders where dietary items of relatively high carbon-nutrient quality represented key forage resources (selective grazers: sable antelope, roan antelope, tsessebe, eland)] and (3) developing a process model where the expected effects of plant metabolic responses to climate on key forage resources were made explicit.

According to the climate–vegetation response model both shorter-term transient temperature acclimation pulses and longer-term shifts in plant metabolic functionality settings were predicted to have occurred in response to temperature trends over the past century. These temperature acclimation responses were expected to have resulted in transient pulses of increased forage availability (increased nitrogen- and carbon-nutrient quality), as well as the progressive long-term decline of the carbon-nutrient quality of forage.

**Conservation implications:** The climate–vegetation response model represents a research framework for further studies contributing towards the enhanced understanding of landscape-scale functioning of savanna systems with reference to the interplay between climate, vegetation and herbivore population dynamics. Gains in such understanding can support sound conservation management.

## Introduction

Herbivore population trends in the Kruger National Park (KNP) over the past century were traditionally explained with reference to decimation by hunting and epizootics (Joubert 2007a; Pienaar 1963), effects of rainfall (Dunham, Robertson & Grant 2004; Owen-Smith & Ogutu 2003; Whyte & Joubert 1988) and predation (Harrington *et al.* 1999; Joubert 2007a, 2007b; Owen-Smith, Mason & Ogutu 2005; Owen-Smith & Mills 2006; Owen-Smith & Mills 2008). However, the long-term and spatially widespread nature of population trends suggested that over-arching landscape-scale influences may also be involved to an as yet unknown extent. A greater role of climate effects as a long-term landscape-scale factor was therefore implicated. Accordingly, we initiated a study to explore the extent to which climate–vegetation responses could plausibly explain diverse and divergent spatiotemporal patterns in population performance of eight large herbivore species, namely African buffalo (*Syncerus caffer*), blue wildebeest (*Connochaetes taurinus*), plains zebra (*Equus burchelli*), waterbuck (*Kobus ellipsiprymnus*), sable antelope (*Hippotragus niger*), roan antelope (*Hippotragus equinus*), tsessebe (*Damaliscus lunatus lunatus*) and eland (*Taurotragus oryx*).

To interpret large herbivore population performance patterns over space and time in relation to climate it was necessary to develop a framework in which the expected effects of climate on

forage quantity and quality were established. Towards this purpose we developed a climate–vegetation response model. This model was developed through interpretation and synthesis of existing knowledge (literature review) and supported by analyses of local patterns of climate effects on forage plant performance and chemical composition. Forage availability to herbivores was taken to be a function of plant productivity and the nutritional quality of the resultant plant material (Fryxell 1991; Holdo, Holt & Fryxell 2009), based on concentrations of protein (nitrogen), non-structural carbohydrates (TNC) and minerals in plant tissues. Key resources for herbivores thus relate to nitrogen productivity, nitrogen quality and carbon-nutrient quality. A central notion of the climate–vegetation response model is that levels of these three forage resource indicators are affected differentially by plant metabolic processes in response to the nature of edaphoclimatic resources (water, temperature and nutrients) available to plants. To the extent that different herbivore species have divergent nutritional requirements in respect of these key forage resources, we expected that their population performances would be affected differentially by conditions of the edaphoclimatic environment (spatial scale) and climate (temporal scale).

The climate–vegetation response model developed here accordingly consists of three main components:

- definition of indicators of forage availability to herbivores (nitrogen productivity, nitrogen quality and carbon-nutrient quality)
- identification of herbivore species guilds of similar nutritional requirements in respect of these indicators
- development of a climate–plant metabolic response process model where the expected effects of plant metabolic responses to climate on key forage resources are made explicit.

With the climate–vegetation response model as explanatory framework, large herbivore population performance patterns in both space and time in the KNP were investigated and interpreted (Seydack *et al.* 2012). In a broader sense, however, our climate–vegetation response model is intended to represent a research framework for further studies contributing towards the enhanced understanding of landscape-scale functioning of savanna systems in respect of the interplay between climate, vegetation and herbivore population dynamics.

## Study area

The KNP is situated in north-eastern South Africa and represents a large (approximately 2 000 000 ha) semi-arid savanna system. The area lies between the Drakensberg escarpment in the west and the Mozambique coastal plain in the east. Covering an altitudinal range of between 200 m a.s.l. and 700 m a.s.l., the KNP falls within two disparate climate zones as defined by the South African Weather Service (Venter, Scholes & Eckhardt 2003). The area north of the Olifants River is in the northern arid bushveld zone, receiving 300 mm – 500 mm rain per year, whilst the southern part of the park falls into the lowveld bushveld zone, with an average annual rainfall of 500 mm – 700 mm

per year. Years of pronounced below-average rainfall were 1963–1964, 1973, 1983–1984, 1987, 1991–1992 and 1998 (Figure 1). Growing season duration (v. Schulze 1997) is on average about 1.5 months shorter in the north than in the south (96 days compared with 142 days, respectively).

Temperature records from stations within or near the KNP followed trends congruent with those recorded globally (Figures 2 and 3). Three phases of temperature increases were discernable. The first reached peak values between 1937 and 1947, followed by a second phase of increasing temperature towards the period 1958–1960 and a third, still ongoing, warming phase which commenced between 1975 and 1978. Locally differentiated temperature trends are shown in Figure 3. Regional temperature lapse rates for monthly means of daily maximum and minimum temperatures are  $-0.777\text{ }^{\circ}\text{C}\times 100\text{ m}^{-1}$  and  $-0.465\text{ }^{\circ}\text{C}\times 100\text{ m}^{-1}$ , respectively (Schulze 1995). As indicated by higher summer-to-winter heat unit differentials (determined according to Schulze 1997), northern areas of the park experience more pronounced temperature seasonality.

The park is longitudinally divided into granitic substrates forming relatively nutrient-poor sandy soils in the west and more nutrient-rich, basalt-derived clay soils in the east (Venter *et al.* 2003). The savanna vegetation on nutrient-poor substrates tends to be dominated by trees of Combretaceae (e.g. *Combretum* and *Terminalia* species) and Caesalpiniaceae, whereas those on more nutrient-rich clay soils are dominated by trees of Mimosaceae (especially *Acacia* species) (Gertenbach 1983; Venter *et al.* 2003). The vegetation of the northern KNP is characteristically dominated by mopane (*Colophospermum mopane*) and this species is well represented in broad-leaved bushveld vegetation types on granites and broad-leaved shrubveld associated with basalts (Gertenbach 1983; Venter *et al.* 2003). The herbaceous layer of the KNP is dominated by  $C_4$  grass species (Kennedy, Biggs & Zambatis 2003) and the more nutrient-rich savanna vegetation types on clay soils carry dense stands of nutritious, high-bulk grasses (Venter *et al.* 2003).

## Materials and methods

### Development of an explanatory framework

Exploration of spatiotemporal patterns in population performance of eight large herbivore species revealed three population performance response groups (i.e. groups of large

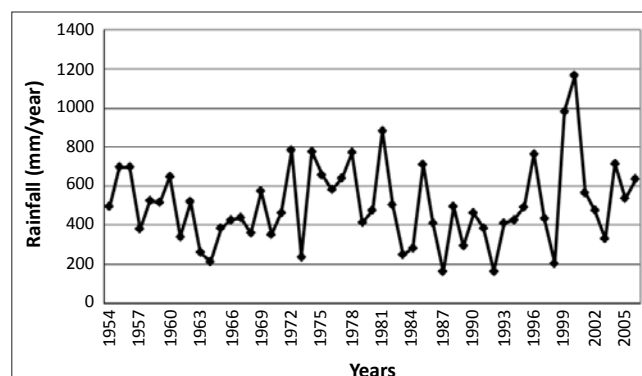
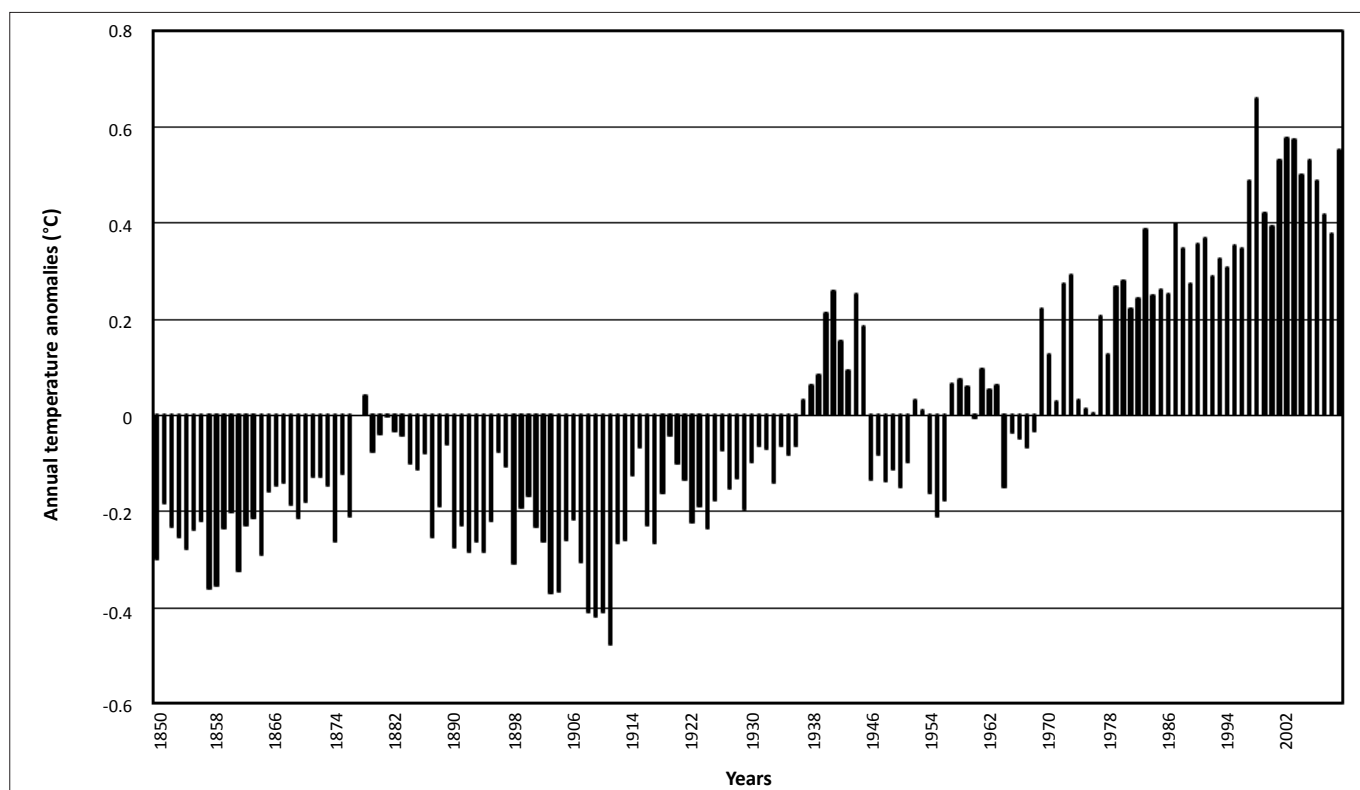


FIGURE 1: Mean annual rainfall in the Kruger National Park (1954–2006).



Graph compiled based on data supplied by P.D Jones, T.J. Osborne and K.R. Briffa, Climatic Research Unit, University of East Anglia and D.E. Parker, Hadley Centre for Climate Prediction and Meteorological Research, Bracknell, United Kingdom.

**FIGURE 2:** Southern hemisphere surface air temperature anomalies between 1850 and 2009.

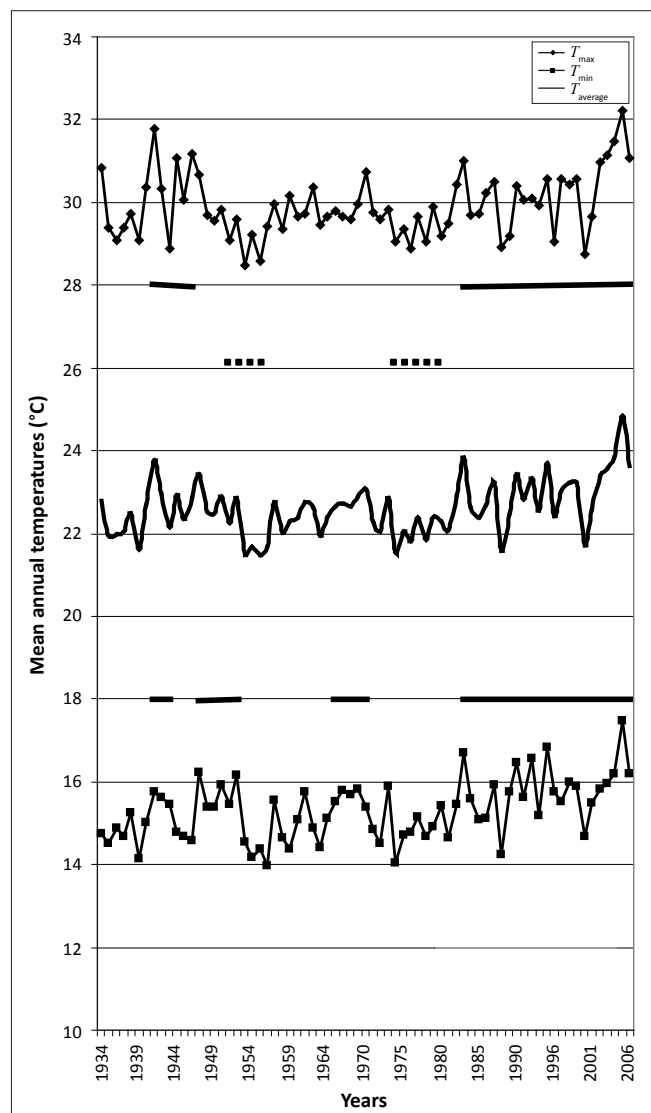
herbivore species that shared broad-scale habitat preferences and similar population performance trends over time) and group-specific correlations with climate variables (Seydack *et al.* 2012). We developed an explanatory framework – the climate–vegetation response model – which permits the interpretation of these correlative patterns in relation to climate effects. As part of the climate–vegetation response model we (1) defined indicators of forage availability (quantity and quality), (2) established forage selection requirements characteristic of and unique to the three herbivore population performance response groups (nutritional guilds), and (3) developed a plant-climate response process submodel. The resulting climate–vegetation response model defined the expected effects of climate on indices of forage availability, thereby providing an explanatory framework for the interpretation of spatiotemporal patterns in herbivore population performance in relation to climate. The model was developed largely based on the interpretation and synthesis of relevant literature. Some results of local research contributed towards the definition of key forage resource indices.

### Definition of indicators of forage quantity and quality

Leaf and stem material of the grass species *Panicum maximum*, *Panicum coloratum* and *Themeda triandra* were collected in and beyond the roan enclosure (Nwashitshumbe, northern KNP) during September 2007, November 2007, August 2008 and February 2009. The apical 20 cm of grass stems were collected as samples of stem material. The samples originated from a study to explore the effects of fire frequency on forage quality,

where sampling was undertaken in four treatment blocks (three inside and one outside of the enclosure) defined by the time since the last burn. Each treatment block contained three sampling localities (replications) to represent a total of 12 samples per sampling event.

The collected grass material was dried at 55 °C overnight and mill ground through a 1-mm sieve to form homogeneous powdered samples. The concentrations of ash minerals and TNC were determined, as well as *in vitro* organic matter digestibility (OMD) of the powdered sample material. These analyses were performed by the Analytical Services department of the Agricultural Research Council (ARC) in Irene. Ashing was performed in a furnace at 600 °C. TNC were analysed as reducing sugars after complete enzymatic hydrolysis to monosaccharides. The method entailed gelatinisation of all starch in the sample by autoclaving, followed by enzymatic hydrolysis of the starch to glucose and determination of glucose content by spectrometric measurement. Duplicate results were within 3% of the mean for each pair. *In vitro* OMD was determined following an adaptation of the two-phase technique described by Tilley and Terry (1963), with some modification introduced by Engels and Van der Merwe (1967). It involved a 24-hour-long fermentation by rumen micro-organisms in a buffer solution followed by a 48-hour-long pepsin digestion after acidification. The reduction in the organic matter content was ascribed to digestion of the sample. For the determination of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , samples were combusted in an automated Thermo1112 Elemental Analyser (Carlo Erba, Milan). The resultant  $\text{CO}_2$  and  $\text{N}_2$  gases were then introduced to a



Horizontal bars denote time spans of three or more consecutive years of above-average mean monthly maximum ( $T_{max}$ ) and minimum ( $T_{min}$ ) temperatures (continuous lines) and three or more consecutive years of below-average  $T_{max}$  (broken line).

**FIGURE 3:** Mean annual temperatures at Musina (525 m a.s.l.), approximately 100 km north-west of the Kruger National Park (South African Weather Service).

Thermo Delta stable light isotope XP mass spectrometer via a continuous flow-through inlet system (Thermo Conflo III).  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  ratios were expressed in the delta ( $\delta$ ) notation in parts per thousand ( $\text{‰}$ ) relative to international standards (Pee Dee Belemnite standard for carbon;  $\text{N}_2$  air for nitrogen). Standard deviations of repeated measurements were less than  $0.1\text{‰}$  for  $\delta^{13}\text{C}$  (Stable Light Isotope Unit, Department of Archaeology, University of Cape Town).

Grass sample collections during November 2007 and February 2009 represented spring and summer sampling events, respectively, and plant growth under conditions of concurrent high levels of temperature and water availability (TW conditions). Dry-season grass and stem material collected during September 2007 had been subject to summer greening in November–December 2006 (TW metabolic cueing at sub-mature stages; mean monthly maximum and minimum temperatures at  $33.9\text{ °C}$  and  $21.1\text{ °C}$ , respectively) and water-stressed summer growth conditions (Tw growth

realisation at mature stages). Dry-season material collected in August 2008 represented conditions following spring greening in September–October 2007 (tw metabolic cueing at sub-mature stages; mean monthly maximum and minimum temperatures at  $30.6\text{ °C}$  and  $17.7\text{ °C}$ , respectively) and summer growth subject to high rainfall conditions (TW growth realisation at mature stages). The main objective of this part of the study was to determine how these varying growth conditions affected the chemical composition and digestibility of the grass tissues and the implications for key indices of forage quality defined in the context of this study.

## Results

### Climate–vegetation response model

#### Indicators of forage availability

**Nitrogen productivity:** Nitrogen productivity is defined as the quantitative availability of forage items for herbivores of a given nitrogen quality (plant protein content) as a result of biomass production. Grass productivity is known to be strongly promoted by water availability [positively correlated with rainfall (Zambatis 2004)] and temperature, especially in the case of tropical grass species (Long 1999; Luo 2007; Wan *et al.* 2005), which have high temperature optima for growth (Dwyer *et al.* 2007; 't Mannetje 1982; Tudsri, Matsuoka & Kobashi 2002; Wilson & Ford 1971). Warming-induced increases in biomass production of  $\text{C}_4$  grasses have been demonstrated under experimental conditions (An *et al.* 2005; Bijoer *et al.* 2008). Accordingly, nitrogen productivity of  $\text{C}_4$  grasses and subtropical woody vegetation is expected to increase over time as ambient temperature increases (Figure 2). However, at progressively higher nitrogen productivity, an inverse relationship to nitrogen quality due to nitrogen dilution is generally encountered (An *et al.* 2005; Fryxell 1991; Fryxell *et al.* 2005; Mutanga *et al.* 2004; Wilson 1982).

**Nitrogen quality:** High nitrogen quality of forage implies high nitrogen concentrations of plant tissues; that is, plant protein content not unduly diluted by structural or non-structural carbon and of relatively high digestibility. An index of nitrogen quality is defined here as the product of nitrogen concentration and OMD of the plant tissues involved. Wet-season nitrogen quality tended to be higher early in the wet season (spring) compared with later in the wet season (summer) (Figure 4c). Nitrogen content in summer leaf material (SUL) was diluted by structural carbon relative to that of spring (SPL) leaf material (analysis of variance for carbon content, followed by a *post hoc* Bonferroni test showed  $\text{SUL} > \text{SPL}$ ;  $p < 0.00001$ ) and carbon-nutrient levels (Figure 4d:  $\text{SUL} > \text{SPL}$ ). This is congruent with nitrogen dilution through growth under conditions of relatively high temperature and water availability (TW conditions), as typically experienced by tropical grasses (Wilson & Ford 1971).

Dry-season leaf (WL) and stem (WS) material were sampled to represent two sets of conditions (Figure 4): summer greening and water-stressed summer growth (WL-Su/WS-Su) and spring greening and summer growth with high rainfall

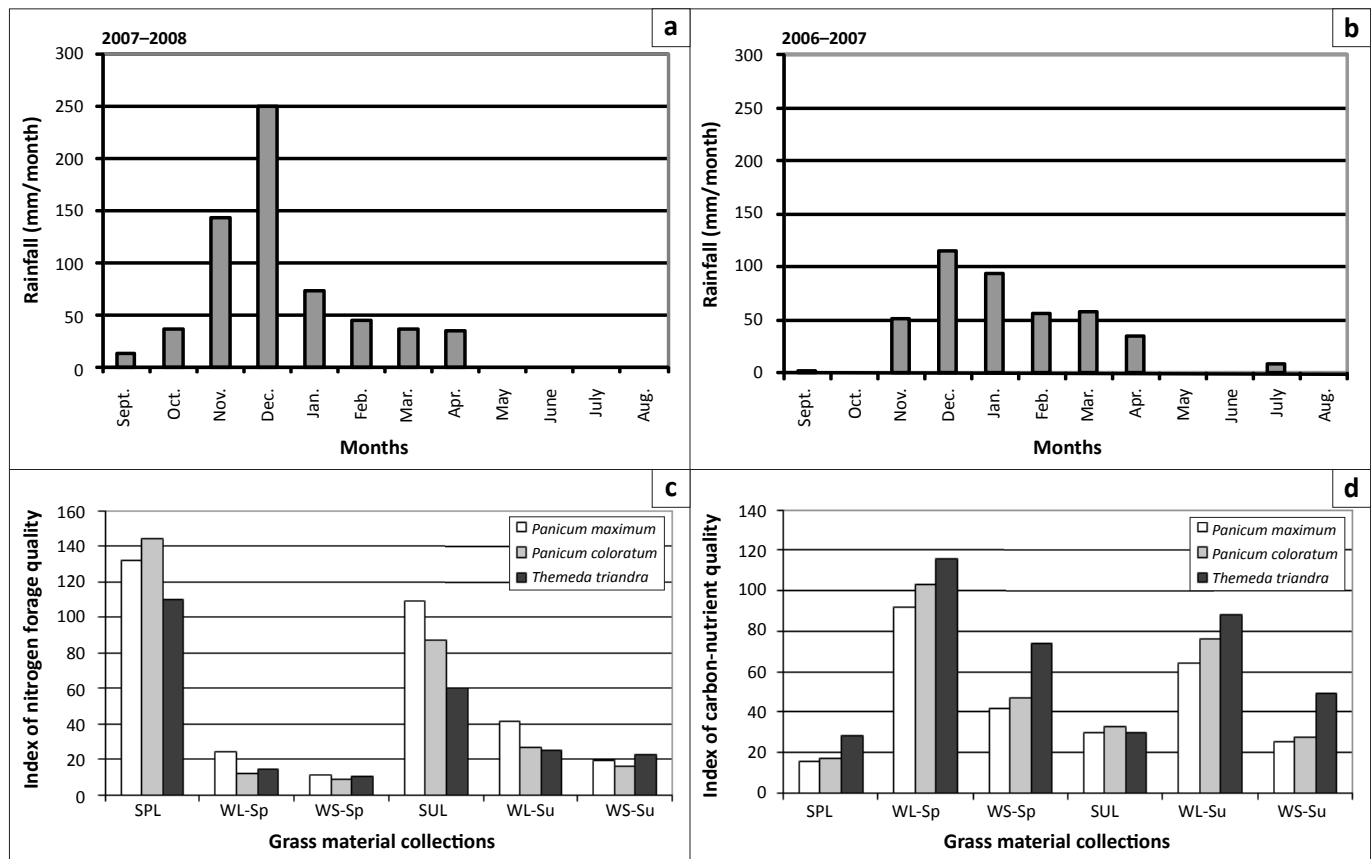


Figure 4 a: Dry-season grass sampling conducted during August 2008 followed spring greening (September/October 2007), but summer growth occurred under conditions of high temperature and water availability (TW conditions).  
 Figure 4 b: Dry-season grass sampling conducted during September 2007 followed summer greening (November/December 2006), but summer growth occurred under relatively dry conditions (Tw conditions).  
 Nitrogen forage quality is defined as the product of nitrogen and organic matter digestibility.  
 Carbon-nutrient forage quality is defined as the product of total non-structural carbon content and ash minerals.  
 SPL, grass leaf material collected in spring (November 2007); WL-Sp, grass leaf material collected in winter (dry season) following spring greening; WS-Sp, grass stem material collected in winter (dry season) following spring greening; SUL, grass leaf material collected in summer (February 2009); WL-Su, grass leaf material collected in winter (dry season) following summer greening; WS-Su, grass stem material collected in winter (dry season) following summer greening.  
**FIGURE 4:** Monthly rainfall at Vlakteplaas (northern basalt plains, Kruger National Park) for two consecutive years (a) 2007/2008 and (b) 2006/2007, and forage quality indices of selected grass tissues (c) index of nitrogen forage quality and (d) index of carbon-nutrient forage quality.

(WL-Sp/WS-Sp), respectively. Nitrogen quality of dry-season WL and WS material (Figure 4c) was enhanced following water-stressed summer growth (WL-Su/WS-Su: Figure 4b; Tw conditions indicated by low  $\delta^{15}\text{N}$  values) compared with such material following summer growth in higher rainfall conditions (WL-Sp/WS-Sp: Figure 4a; TW conditions indicated by high  $\delta^{15}\text{N}$  values; N-quality: leaf material:  $F = 113.36, n = 72, p < 0.000001$ ; stem material:  $F = 50.77, n = 72, p < 0.000001$ ). OMD of dry-season grass tissue (both leaf and stem material) following water-stressed summer growth (Tw conditions; Figure 4b) was significantly higher than of dry-season material following summer growth under TW conditions (Figure 4a; OMD: ANOVA: Bonferroni *post hoc* test: WL-Su > WL-Sp;  $p < 0.0001$ ; WS-Su > WS-Sp:  $p < 0.00001$ ). OMD of dry-season grass leaf material was positively related to nitrogen content and negatively correlated with  $\delta^{15}\text{N}$  values (multiple regression of OMD on N and  $\delta^{15}\text{N}$ :  $\beta$  of N = +0.758;  $\beta$  of  $\delta^{15}\text{N}$  = -0.348,  $R^2 = 0.42, n = 72$ ). According to the results of Codron *et al.* (2005) seasonal shifts in plant  $\delta^{15}\text{N}$  corresponded positively with seasonal summer rainfall, supporting our interpretation that  $\delta^{15}\text{N}$  values index summer growth activity under TW conditions. These relationships are consistent with general

findings that metabolic activity under water stress promotes digestibility (Wilson 1982) and that high growth activity under TW conditions results in reduced forage quality. Metabolic activity under conditions of high temperature and water availability (TW conditions) is expected to negatively affect dry matter digestibility as it promotes more rapid growth and stem development of, particularly, tropical grasses ('t Mannetje 1975; Wilson 1982; Wilson, Taylor & Dolby 1976). High growth temperatures also hasten the maturation of individual tissues and the digestibility of plant tissue is usually higher when grown at low temperatures, such as in spring or winter ('t Mannetje 1984; Wilson 1982).

**Carbon-nutrient quality:** Carbon-nutrient quality of forage items is defined here as the product of TNC and ash mineral concentrations (Figure 4d). Dry-season TNC content of grass leaf material following spring greening was significantly higher than that of leaf material following summer greening (dry-season TNC content: WL-Sp > WL-Su;  $F = 25.02, p < 0.00001$ ). A similar pattern was found for ash (mineral) contents (ANOVA, followed by *post hoc* Bonferroni test: WL-Sp > WL-Su and WS-Sp > WS-Su,  $p < 0.00001$ ). These results are consistent with a metabolic response mode

of low-temperature growth during spring (tw metabolic cueing at sub-mature stages) resulting in storage allocation of TNC (Estiarte & Peñuelas 1999; Herms & Mattson 1992; Wilson 1975) and of minerals (Balasko & Smith 1971). In accordance with these findings, high carbon-nutrient quality was typically encountered in dry-season leaf material (Figure 4d) and was higher in dry-season leaf and stem tissue in grass cohorts that had been subject to spring greening (Figure 4d; ANOVA followed by a *post hoc* Bonferroni test: WL-Sp > WL-Su,  $p < 0.00001$ ; WS-Sp > WS-Su,  $p < 0.00001$ ). Carbon-nutrient quality forage items are thus characterised by relatively high concentrations of TNC and ash minerals resulting from substantial metabolic allocation to storage under circumstances promoted by constrained growth (particularly owing to low temperatures, but also moisture stress: tw conditions) but sustained photosynthesis.

Carbon-nutrient quality of dry-season plant leaf and stem material of *T. triandra* (Andropogoneae) was generally higher than for the two species of Paniceae (Figure 4d; ANOVA and *post hoc* Bonferroni tests:  $p < 0.01$ ). This reflected the predisposition of andropogonoid species, geared to cope with more pronounced seasonality (Osborne 2008), towards greater metabolic scope for storage investment. The typical accumulation of tannin-like substances in the foliage of Andropogoneae indicates a carbon excess metabolism with pronounced allocation to storage (Baas 1989; Herms & Mattson 1992). Such physiological characteristics are considered adaptive to ensure sustained metabolic performance under seasonally variable conditions of resource availabilities (temperature and water: tW/Tw/tw conditions). All species of Andropogoneae function according to the NADP-ME biochemical subtype and these are implicated to operate at lower temperature optima than species of the other subtypes, including, *inter alia*, species of Paniceae (Ehleringer, Cerling & Helliker 1997). Grass species of this biochemical subtype, and particularly of Andropogoneae, also exhibited the smallest responses to changes in environmental conditions (Buchmann *et al.* 1996). These findings are suggestive of the capacity of Andropogoneae species for sustained metabolic performance at variable and lower resource levels (dry-season growth), underpinning their metabolic scope for storage of metabolites (TNC and minerals for enhanced carbon-nutrient quality).

### Herbivore species guilds of key nutritional requirements

In this section we present evidence suggesting that herbivore species within particular population performance response groups share similar broad-scale forage selection requirements. Buffalo and waterbuck are considered roughage feeders able to digest fibrous food relatively efficiently (Hofmann 1973, 1989). Despite the relatively unselective bulk grazing habit of buffalo, they adjust their feeding patterns in relation to seasonally changing forage quantity and quality (Macandza, Owen-Smith & Cross 2004). However, for both these species food quantity seems to override exacting quality requirements. This is in contrast to blue wildebeest and zebra, which have clear preferences

for short-grass areas on nutrient-rich soils (Grange & Duncan 2006; Traill 2004). Both species select grass patches of high nitrogen quality for feeding, although zebra, as a hindgut fermenter, can tolerate more fibrous and longer-grass feeding conditions (Bodenstein, Meissner & Van Hoven 2000; Smuts 1972).

Apart from species-specific, often seasonally changing, feeding preferences (Dunham *et al.* 2004; Heitkönig & Owen-Smith 1998; Joubert & Bronkhorst 1977; Magome *et al.* 2008; Watson & Owen-Smith 2000), all four selectively feeding species (i.e. tsessebe, eland, sable and roan antelope) are able to adapt to a wide range of grass heights and often include medium to tall grasses in their diets (Joubert 1976; Skinner & Chimimba 2005; Traill 2004). According to a study by Parrini (2006) sable antelope do not avoid stemmy grass tufts and include tall stemmy species generally avoided by short-grass grazers. Sable antelope were found to be particularly tolerant of stems in habitats with intermediate to high nutrient levels. Heitkönig and Owen-Smith (1998) found a similar pattern in roan antelope, which tolerated stems when leaf quality was high. The preferred feeding sites of tsessebe typically have soils with a high clay content (Dörgeloh 2006). Topi (*Damaliscus lunatus jimela*), with foraging habits believed to be similar to those of tsessebe, selected for the tallest plants and species with relatively long leaves when feeding on grass with more than 20% green leaves (Duncan 1975 op. cit. Parrini 2006). These patterns of ingesting stem material together with leaf matter and the relatively high importance of nutrient contents of these are commensurate with the maintenance of relatively high dietary TNC and mineral nutrient levels resulting in carbon-nutrient ratios as required for sustained carbon-nutrient quality.

Numerous studies have revealed the prominence of andropogonoid grass species in the preferred habitat and forage species assemblages of sable antelope (Le Roux 2010; Magome 1991; Parrini 2006), roan antelope (Joubert 1976; Van Lavieren & Esser 1979), tsessebe (Gureja & Owen-Smith 2002) and eland (Watson & Owen-Smith 2000). As indicated in the previous section, andropogonoid grass species would tend towards a sustained metabolic performance type metabolism and thus have a propensity towards carbon and nutrient storage, particularly when subject to seasonally low temperature conditions. Under such metabolically favourable conditions, these species are expected to have high carbon-nutrient quality; that is, a combination of favourable levels of TNC, nitrogen and minerals. All these features of forage selectivity, including tolerance of stemminess, prominence of andropogonoid grass species, adaptability to a wide range of grass heights and, in the case of browsing, feeding on freshly fallen TNC-rich leaves [see Skinner & Chimimba (2005) for reference to eland] indicate that these species can be classed as selective feeders of plant parts of relatively high carbon-nutrient quality. In summary, the eight species studied here are grouped into three guilds of nutritional requirements: bulk feeders with tolerance to fibrous herbage (buffalo and waterbuck), bulk feeders with preference for high nitrogen

quality (short-grass grazers: blue wildebeest and zebra) and selective feeders for which dietary items of relatively high carbon-nutrient quality are of particular importance (selective grazers: sable antelope, roan antelope, tsessebe and eland).

### Plant–climate response processes

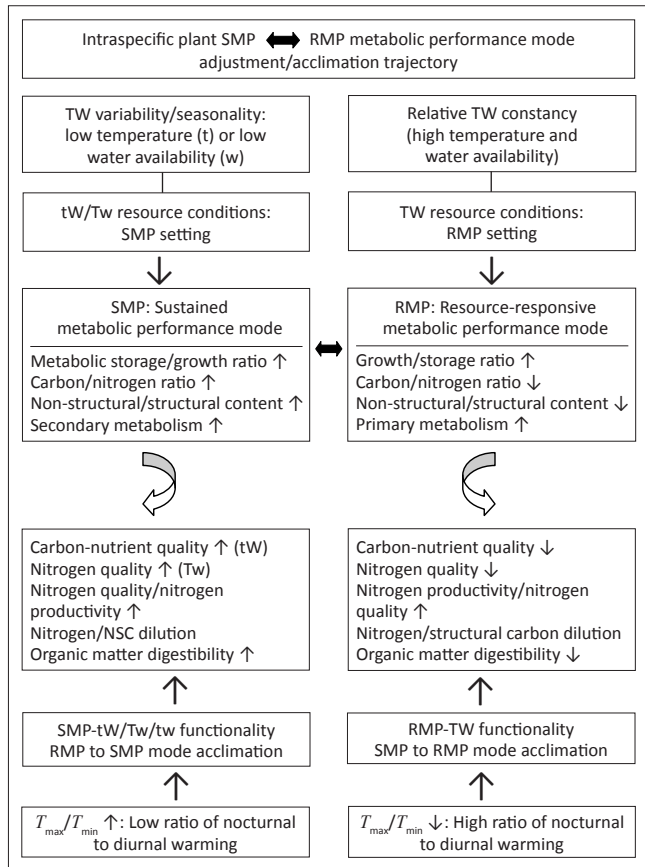
**Plant metabolic performance trade-off relationships:** Owing to resource limitations plants are subject to trade-offs between growth, maintenance, storage, reproduction and defence (Herms & Mattson 1992). Consequently, there are, *inter alia*, strong inverse relationships between the functional allocation to growth and non-growth processes, notably carbon storage (Herms & Mattson 1992). Accordingly, there is an allocation trade-off between quantity of plant tissue produced through growth (structural plant content) and quality, represented by the proportion of non-structural plant content (metabolically active components and storage products). Thus, abundance of resources such as water, nutrients and temperature enhance productivity, but increasing productivity then progressively reduces plant tissue quality for herbivores through nutrient dilution (An *et al.* 2005; Dwyer *et al.* 2007; 't Mannetje 1982, 1984; Tudsri *et al.* 2002; Van Soest, Mertens & Deinum 1978; Wilson & Ford 1971; Wilson 1982), reduction in digestibility ('t Mannetje 1975, 1984; Van Soest *et al.* 1978; Wilson & Ford 1973; Wilson & 't Mannetje 1978) and reduced allocation to storage (low TNC content) (Estiarte & Peñuelas 1999; Herms & Mattson 1992; Van Soest *et al.* 1978).

The climate–vegetation response model was developed to integrate existing knowledge and to form part of an explanatory template for spatiotemporal patterns of climate–vegetation response processes controlling forage quantity and quality. At the core of this model is the metabolic performance trade-off model, from which predictions can be made regarding divergent plant responses to site and climate-linked resource constraints and their impact on parameters of forage availability to herbivores. The principal trade-off in the context of this model is between maximised peak performance, closely tracking and responsive to conditions of resource surplus (RMP; resource responsive metabolic performance mode), and sustained performance when subject to conditions of varying resource levels or deficits (SMP; sustained metabolic performance mode). The capacity for maximum metabolic performance under conditions of resource surplus is at the cost of the capacity for sustained performance under conditions of resource deficits or fluctuations. In line with this reasoning, we expect a propensity towards the RMP mode under conditions of high and less fluctuating levels of temperature and water availability (TW conditions: combination of relatively high and sustained levels of water and temperature during the growing season), whereas under conditions of fluctuating resource levels and pronounced deficits (regarding temperature and water; tW or Tw conditions), the SMP mode would be expected to predominate.

High peak-level performance characteristics of the RMP mode require high turnover metabolism (capacity for high

instantaneous rates of photosynthesis;  $A_{max}$ ). This is generally associated with high foliar nitrogen levels (Lambers, Chapin & Pons 1998) resulting in increased nitrogen/carbon ratios of plant tissues. In contrast, sustained performance capacity of the SMP mode requires resource use efficiency and is associated with the propensity towards somatic accumulation [size, storage, longevity: relatively high carbon/nitrogen ratios of plant tissues; Herms and Mattson (1992)]. Furthermore, stress-tolerant plants (SMP mode) tend to allocate an especially high proportion of available energy to maintenance respiration required to tolerate adverse environmental conditions (Taylor 1989). Plants in a relative SMP mode are accordingly expected to be even more sensitive to resource conditions inducing elevated maintenance respiration, such as increased mean minimum temperature (reflecting nocturnal temperature conditions) ( $T_{min}$ ). Resource constraints on growth are generally more intense than their inhibitory effect on photosynthesis. As a consequence of carbon acquisition exceeding growth requirements, the products of photosynthesis accumulate, primarily as carbohydrate storage products (Baas 1989; Herms & Mattson 1992; Lambers & Poorter 1992). When tracking resource surplus conditions favourable for both photosynthesis and growth in RMP-mode plants, the resource-level response relationships for growth and photosynthesis tend to be similar (Wilson & Ford 1973). In SMP-mode plants, stress tolerance capacity is associated with photosynthesis being relatively less sensitive to resource levels than growth. Accordingly, there is greater scope for source (photosynthesis) to sink (growth) imbalance in SMP-mode plants, favouring allocation to secondary metabolism and storage as carbon assimilation levels exceed those which are required for growth. Plants in relative SMP mode are thus comparatively stress tolerant in order to cope with fluctuations in resource levels. As such their metabolism is capable of functioning at relatively low temperature and water availability levels/optima (broad metabolic amplitude; SMP-tw functional efficiency). Such metabolic capacity is, however, associated with relatively high storage-to-growth allocation priority and comparatively high maintenance respiration costs (i.e. temperature sensitivity). In contrast, plants in relative RMP mode are geared to the maximum use of resource surplus conditions, functioning at relatively high temperature and water resource level optima (narrow metabolic amplitude) and high growth-to-storage priority (Figure 5).

**Plant metabolic performance mode settings:** The relative expression of SMP to RMP mode functionality/acclimation is a function of the combined availability levels of temperature and water (TW resource conditions). The higher the concurrent and uninterrupted levels of temperature and water available to plants, the more pronounced the intraspecific metabolic adjustment towards higher RMP mode functionality settings. The relative expression of SMP or RMP depends on the spatiotemporal nature of resource availability for plants (water and temperature resource levels and variability or seasonality), shaping forage quantity and quality as a



T/t and W/w denote relatively high or low levels of temperature and water availability, respectively.

C, carbon; N, nitrogen; NSC, non-structural carbon;  $T_{max}$ , mean periodic maximum temperature;  $T_{min}$ , mean periodic minimum temperature.

**FIGURE 5:** Sustained metabolic plant performance (SMP) to resource-responsive metabolic performance (RMP) mode adjustments to resource conditions, also representing the SMP to RMP temperature acclimation trajectory endpoints (climate–vegetation response process model).

consequence of the relative prevalence of SMP-tW/Tw to RMP-TW functionality (Figure 5). Resource conditions in the northern KNP are characterised by greater moisture stress levels and higher degrees of resource level fluctuations regarding both moisture availability and temperature compared to the southern KNP (increasing north to south rainfall gradient: KNP-north = 483 mm/year; KNP-central = 535 mm/year; KNP-south = 632 mm/year). Growth season duration (v. Schulze 1997) is, on average, about 1.5 months shorter in the northern KNP. According to the metabolic performance trade-off model, we therefore expect the SMP mode to predominate (intraspecifically) in northern KNP areas and the RMP mode to be more prevalent in southern areas of the park. Conditions prevailing in the central KNP are expected to promote an intermediate position in this regard. Conditions for plant functionality are also expected to change along an altitudinal gradient [temperature lapse rates for monthly means of daily maximum and minimum temperatures are  $-0.777\text{ }^{\circ}\text{C}\times 100\text{ m}^{-1}$  and  $-0.465\text{ }^{\circ}\text{C}\times 100\text{ m}^{-1}$ , respectively (Schulze 1995)]. A pattern of lower temperatures and increased rainfall at higher altitudes represents tW conditions, with Tw conditions prevailing at lower altitudes. Combining the north–south water availability and altitudinal temperature gradients, plant functionality settings were

identified and the associated expected implications for forage quality indicated in accordance with the metabolic performance trade-off model (Table 1).

As a general notion, nitrogen quality is usually considered to be higher in plants on nutrient-rich geological substrates, resulting in higher palatability for herbivores (Skidmore *et al.* 2010; Venter *et al.* 2003). This pattern may, however, be modified at various spatial scales by the availability of water (Mutanga *et al.* 2004) and factors resulting in nitrogen dilution (accentuated SMP or RMP functional expression as in northern and southern KNP, respectively). At a spatial scale we thus generally expect the prevalence of relatively high nitrogen quality forage on nutrient-rich geological substrates in the central KNP (Table 1).

**Temperature acclimation and forage quality:** Ambient temperature has been increasing over the past century (Figure 2). In particular,  $T_{min}$ , which represents nocturnal temperature conditions, has increased more steeply than the mean periodic maximum temperature ( $T_{max}$ ), which represents diurnal temperature conditions (Houghton *et al.* 1996). Increasing  $T_{min}$  is expected to stimulate nocturnal maintenance respiration (Wan *et al.* 2009), promoting temperature acclimation in order to restore the original steady-state respiration-to-photosynthesis ratio (Dewar, Medlyn & McMurtrie 1999). As temperature increases, leaf metabolic pools adjust until the original steady-state respiration-to-photosynthesis ratio is re-established. Leaf labile carbon, starch and protein pools decrease in response to increased temperature, eventually reaching a new, lower steady state, consistent with the general pattern of plant carbohydrate and soluble protein content being negatively correlated with growth temperature (Dewar *et al.* 1999; Wan *et al.* 2009). These acclimation responses represent intraspecific SMP to more RMP functionality shifts (SMP-to-RMP temperature acclimation). This has consequences for forage quality, such as reduced carbohydrate and mineral storage levels (progressively lowered carbon-nutrient quality) and reduced nitrogen quality due to nitrogen dilution and lowered digestibility resulting from high RMP mode-based growth rates (Figure 5).

In the climate–vegetation response model the expression of relative RMP to SMP functionality results from, *inter alia*, the acclimation to changing temperature conditions. In response to increasing  $T_{max}$  (daytime temperatures), the productivity of tropical and subtropical forage plants (especially  $C_4$  grasses) is increased (Long 1999; Luo 2007; Wan *et al.* 2005), resulting in greater quantities of plant protein in the landscape (increased nitrogen productivity).  $T_{max}$  was found to be positively correlated with  $T_{min}$  ( $r = 0.52$ ,  $n = 30$ ,  $p < 0.004$ ) and negatively correlated with the amounts of summer rainfall ( $r = 0.54$ ,  $n = 30$ ,  $p < 0.003$ ). Phases of relatively elevated  $T_{max}$  therefore indicate conditions of increased solar radiation (reduced cloud cover) and reduced water availability for plant growth (reduced rainfall). The associated increased photosynthesis-to-growth ratio is conducive to enhanced





**TABLE 1:** Plant functionality settings according to prevailing environmental conditions in various parts of the Kruger National Park and their expected consequences for forage quality (climate–vegetation response model).

Area of KNP (bold) and CN/N quality status	Altitude (m a.s.l.)	MAP (mm)	Modes of plant functionality (bold) and reasons for forage quality status
<b>KNP-North (upper altitudes)</b>	400–500	500	<b>SMP-tW</b>
CN quality: high	–	–	Low temperature SMP productivity
N quality: compromised	–	–	Nitrogen dilution through non-structural carbon content of plant tissues
<b>KNP-North (lower altitudes)</b>	300–400	450	<b>SMP-Tw</b>
CN quality: compromised	–	–	Due to functionality at relatively high temperatures
N quality: moderate	–	–	Growth curbed by moisture stress; some N dilution through non-structural carbon content of plant tissues
<b>KNP-Central (upper altitude)</b>	350–500	550	<b>Intermediate RMP-SMP</b>
CN quality: variable	–	–	Favourable where SMP-tw conditions prevail
N quality: high	–	–	High where growth is curbed by moisture stress; on nutrient-rich sites
<b>KNP-Central (lower altitude)</b>	150–350	500	<b>Intermediate RMP-SMP-Tw</b>
CN quality: compromised	–	–	Due to functionality at relatively high temperatures
N quality: high	–	–	Growth curbed by moisture stress i.e. constrained TW growth; on nutrient-rich sites
<b>KNP-South (upper altitude)</b>	500–700	700	<b>RMP-tW</b>
CN quality: moderate	–	–	Comparatively low temperatures due to altitude, especially on south-facing aspects, and comparatively high dry season rainfall support CN quality
N quality: low	–	–	Nitrogen dilution through structural carbon content
<b>KNP-South (mid/lower altitude)</b>	300–500 150–300	600	<b>RMP-Tw</b>
CN quality: low	–	–	RMP mode functionality at relatively high temperatures leaving reduced scope for storage based metabolism
N quality: high	–	–	Supported under conditions of low wet season and high dry-season rainfall; on nutrient-rich sites

T/t and W/w denote availability and functionality at relatively high or low levels of temperature and water availability, respectively.

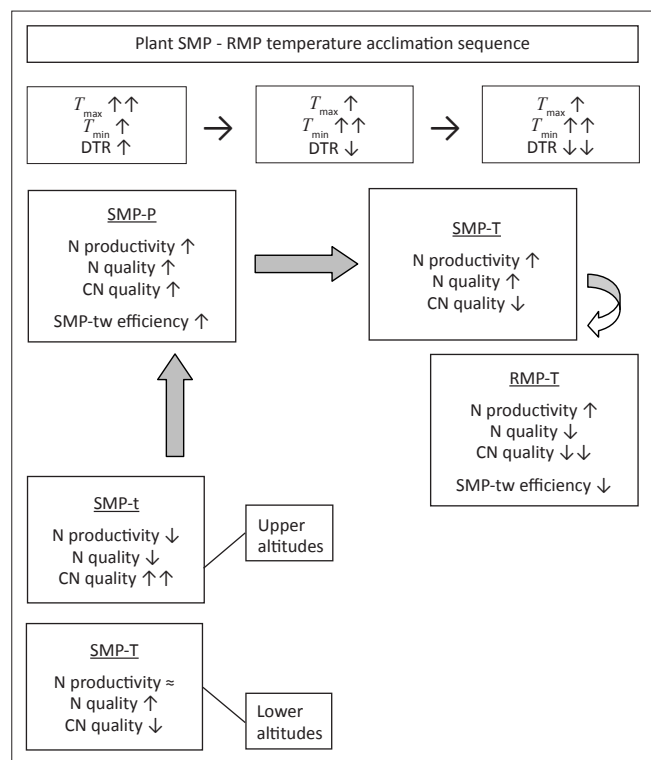
KNP, Kruger National Park; MAP, mean annual precipitation; SMP, sustained metabolic plant performance; RMP, resource-responsive metabolic plant performance modes; N, nitrogen; CN, carbon-nutrient.

forage quality (increased storage allocation; reduced nitrogen dilution). During the initial phases of increasing temperature,  $T_{max}$  is relatively high compared with  $T_{min}$  and relatively high diurnal temperature ranges are thus encountered, supporting a pulse of enhanced SMP productivity (increased  $T_{max}/T_{min}$  ratio, increased  $T_{max} - T_{min}$  differential, and increased ratio of photosynthesis to respiration). This forms the basis of the first of four defined temperature acclimation phase states (SMP-P, phase of increased SMP productivity) constituting the temperature acclimation sequence resulting from (pulses of) increasing atmospheric temperature (Figure 6). However, as the  $T_{max}/T_{min}$  differential (diurnal temperature range; DTR) declines as nocturnal warming ( $T_{min}$ ) increases faster than daytime temperatures, SMP-to-RMP mode acclimation occurs (decreased  $T_{max}/T_{min}$  ratio, decreased  $T_{max} - T_{min}$  differential, and increased ratio of respiration to photosynthesis) and sequential temperature acclimation phase states come into effect (Figure 6). The initially enhanced SMP mode productivity declines and RMP-mode growth increases [referred to as over-compensation by Wan *et al.* (2009)]. The associated shift from SMP-tW/Tw to RMP-TW functionality has physiological consequences which compromise forage quality (Figure 5), notably owing to a shift from storage-based to relative growth-dominated metabolism. This results in a reduction of stored metabolites (TNC, minerals and protein) relative to the accumulation of structural carbon through accelerated growth (reduced carbon-nutrient quality; Figure 5). Furthermore, RMP-TW mode functionality implies metabolic growth activity at higher water and temperature optima. Growth realisation thus takes place under conditions of concurrently high temperature and water availability (TW conditions; at high water and temperature optima), constraining plant productivity under conditions when

growth-curbed physiological activity (based on SMP-tw functional efficiency) associated with the production of high-quality forage (early morning hours, early in season, dry season growth: SMP-tw functionality) could have occurred. Dry-season rainfall supports SMP-tw functionality, thus promoting the production of forage items of high carbon-nutrient and nitrogen quality (Figure 5). However, with progressive SMP-to-RMP acclimation SMP-tw efficiency is expected to decline as RMP-TW functionality favours growth under conditions of higher temperature and water availability. SMP-to-RMP temperature acclimation (shifts from SMP-tW/Tw/tw to RMP-TW functionality) is therefore expected to result in forage with lower nitrogen quality (Figure 5: nitrogen dilution and lowered dry-season forage digestibility) and notably lower carbon-nutrient quality (Figure 5: low metabolic storage allocation priority).

**Spatiotemporal interactions in temperature acclimation and functionality settings:** Following from the climate–vegetation response patterns postulated under the climate–vegetation response model we expect pulses of increased forage availability induced by pseudo-cyclic temperature increases and progressive long-term shifts towards increased RMP functionality settings.

- Pulses of increased forage availability due to increased productivity of quality forage induced by pseudo-cyclic pulses of temperature increases (Figure 2 and 3: increasing towards 1940; increasing towards 1960; increasing after 1975): In response to transient rising  $T_{max}$  pulses of SMP productivity (SMP-P temperature acclimation phase state) occur when the temperature optima for plant functionality are still relatively low (tw metabolic activity). However, as acclimation to  $T_{min}$  takes effect, increased RMP-TW



CN quality, carbon-nutrient quality; DTR, diurnal temperature range; N, nitrogen; T/t or W/w, plant functionality at relatively high or low temperature or water availability levels, respectively;  $T_{max}$ , mean periodic maximum temperature;  $T_{min}$ , mean periodic minimum temperature.

**FIGURE 6:** Sustained metabolic performance (SMP) to resource-responsive metabolic performance (RMP) mode temperature acclimation sequence involving four phase states: an initial SMP productivity pulse (SMP-t/SMP-P → SMP-P) followed by temperature acclimation (SMP-t/SMP-P → SMP-T → RMP-T) along the SMP-RMP acclimation trajectory (Figure 5) of intraspecific plant metabolic responses to temperature variables.

metabolic activity of plants results in reductions in forage quality and thus forage availability (Figure 6).

- Progressive long-term shifts towards relatively advanced RMP functionality settings in response to cumulative acclimation to  $T_{min}$  and declining diurnal temperature ranges: Trends of progressively deteriorating carbon nutrient quality and increasing nitrogen productivity-to-nitrogen quality ratios (Figure 5) over the past century were accordingly anticipated (Figure 2).

Owing to higher and more predictable levels of water availability to plants, such long-term shifts towards higher RMP functionality settings would have taken effect earlier (see Figures 2 and 3, notably in response to prolonged temperature increases between approximately 1930 and 1940–1945) and to more advanced RMP settings in the southern KNP (Table 1). Furthermore, as plants are already functioning at higher RMP settings in the southern KNP, SMP–RMP–SMP temperature response pulses (Figure 6) are expected to be attenuated relative to those in the northern KNP, where pronounced associated pulses of forage availability are expected to be encountered.

## Discussion

### Model postulates and predictions

The postulates and predictions inferred from the climate-vegetation response model represent an explanatory

framework geared to permit, *inter alia*, the interpretation of herbivore population performance patterns in space and over time. Based on the postulates of this model inferences can be made as to how the metabolic responses of plants to their dynamic edaphoclimatic environment shape forage availability for herbivores by affecting the levels of key forage resources (relating to nitrogen productivity, nitrogen quality and carbon-nutrient quality).

### Key forage resources

The climate-vegetation response model differentiates three key indicators affecting forage availability to herbivores: nitrogen productivity, nitrogen quality and carbon-nutrient quality. Nitrogen productivity refers to the quantitative availability of forage items for herbivores of a given nitrogen quality (plant protein content) as a result of biomass production. High nitrogen quality of forage implies high nitrogen concentrations of plant tissues; that is, plant protein content not unduly diluted by structural or non-structural carbon and of relatively high digestibility. Carbon nutrient quality forage items are characterised by relatively high concentrations of non-structural carbohydrates and ash minerals resulting from metabolic allocation to storage under circumstances promoted by constrained growth (low temperatures, moisture stress: tw conditions), but sustained photosynthesis. Levels of these key forage resource indicators in plants (referring primarily to  $C_4$  grasses) are determined by plant metabolic responses to the spatiotemporally dynamic availability of resources (temperature, water and nutrients; Figure 5).

### Herbivore species guilds of nutritional requirements

As inferred from the nature of the diets of eight large savanna herbivore species, three herbivore species guilds of nutritional requirements were identified: bulk feeders with tolerance to fibrous herbage (buffalo and waterbuck), bulk feeders with preference for high nitrogen quality forage (short-grass grazers: blue wildebeest and zebra) and selective feeders for which dietary items of relatively high carbon-nutrient quality represent key forage resources (selective grazers: sable antelope, roan antelope, tsessebe and eland).

### Spatial distribution of key forage resources

Plant metabolic adjustments to the north–south water availability and altitudinal temperature gradients are expected to determine the spatial distribution of SMP to RMP functionality settings across the KNP (Table 1). The general pattern involved higher SMP functional expression in the drier, northern areas of the park and at higher altitudes, and advanced RMP functionality settings towards the south. As the SMP mode involves relatively growth-curbed, storage-based metabolism, the availability of forage of enhanced carbon-nutrient quality is accordingly expected to be higher in the northern KNP and at higher altitudes. Metabolic performance responses of intermediate SMP–RMP modes favour lower levels of nitrogen dilution and are associated with forage of relatively high nitrogen quality, especially of plants on nutrient-rich geological substrates (Table 1: central KNP).



### Climate-driven temporal trends in forage availability

According to the climate–vegetation response model, both shorter-term transient temperature acclimation pulses (Figures 2 and 3: increasing temperature towards 1940; increasing towards 1960; increasing after 1975 ) and longer-term shifts towards advanced RMP functionality settings are predicted to have occurred in response to temperature trends over the past century (Figure 2). These temperature acclimation responses are expected to have resulted in transient pulses of increased forage availability (increased nitrogen and carbon-nutrient quality; Figure 6), as well as the progressive long-term decline of carbon-nutrient quality of forage and an increasing nitrogen productivity/nitrogen quality ratio associated with advanced RMP functionality settings (Figure 5).

### Spatiotemporal interaction in forage availability

Accentuated temperature acclimation responses (Figure 6) are predicted for circumstances where low and unpredictable water availability favour the prevalence of SMP mode settings; that is, in northern relative to southern KNP. More pronounced associated effects on nitrogen quality and carbon-nutrient quality are thus expected towards the northern areas of the park, with attenuation or absence of such responses where relatively high RMP functionality settings already predominate towards the southern KNP.

## Conclusion

The climate–vegetation response model as outlined here was applied as an explanatory framework with respect to herbivore population performance patterns in the KNP. Such application resulted in the internally consistent interpretation of spatiotemporal patterns of large herbivore population performance in relation to climate (Seydack *et al.* 2012).

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### Competing interests

The authors declare that they have no financial or personal relationship(s) which may have inappropriately influenced them in writing this paper.

### Authors' contributions

A.H.S. (Garden Route National Park) was responsible for conceptualising and developing the climate–vegetation response model. C.C.G. (Kruger National Park), I.P.S. (Kruger National Park) and N.Z. (Kruger National Park) contributed to in-depth discussions through sharing their knowledge of animal and plant ecology pertaining to the KNP. W.J.V. (Garden Route National Park) acted as field project leader of the research into climate effects on forage quality and J.B. (Garden Route National Park) was involved in data processing.

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