Drought impact on plant nutrients in a semi-arid rangeland and its implications for sustaining wild herbivores

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Abstract

The impacts of drought on the nutritive value of natural forage and the implications thereof for sustaining herbivores are not well understood. Most studies have shown that drought-induced stress reduces plant nutrient concentrations. The consequential declines in forage quality of rangeland may be an important limiting factor in sustaining wild herbivore populations through periods of drought. In the semi-arid southern Kalahari of South Africa, the 2014-2020 drought resulted in high plant and herbivore mortalities. This study aimed to determine if the drought resulted in nutrient deficient forage, therefore contributing to the declines observed in herbivores. For this, the nutrient content of the most abundant woody and grass species was determined during the drought and the first wet year following the drought. The impact of drought differed markedly between dicot woody species and monocot grasses. In the former, crude protein concentrations were reduced while macro nutrient concentrations were elevated. In the latter, crude protein contents were elevated, and the content of most macro nutrients reduced. Importantly, the drought did not result in nutrient deficient forage. The drought resulted in a prolonged dry season, when forage quantities and nutritive value of plants were naturally at their lowest,. It was concluded that the extension of the dry season was the main cause of herbivore mortalities.

Keywords: plant nutrients, forage, herbivores, nutrient deficiencies

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1. Introduction

The effect of droughts in semi-arid environments on plant growth, survival and recruitment has been well documented (e.g. Knapp et al. 2017; Bodner and Robles 2017, Milton et al. 2023). Less known is the potential impact of drought stress on the nutritional status of the plants within these ecosystems. Water stress (i.e. drought) influences physiological processes within plants, even on a molecular level (Kumar et al. 2021). Many of these processes, such as photosynthesis, stomatal activity, and transpiration are involved in the assimilation and uptake of nutrients from the soil (Cramer et al. 2009; Waraich et al. 2011). As a result, droughts can also influence the concentration of nutrients in plants (Fierer and Schimel 2002; Sanaullah et al. 2012). The extent to which climatic conditions, such as drought, influence plant nutrient concentrations is likely to vary between species and regions. Other factors, such as soil properties, plant age and grazing are also known to determine plant species' nutrient concentrations (Stapelberg et al. 2008). The mineral content of plants is also directly related to the mineral content of the soil they grow in (Underwood and Suttle 1999). Furthermore, the nutrient concentration may not only differ between plant species but also between plant parts. It may also vary considerably during seasonal cycles and the life stage of the plant (Owen-Smith 1979). It is known for example that in many species the crude protein content naturally declines as plant matures (Meissner et al. 1999; Smit 2007). Given the numerous variables and the complexities of the processes that ultimately determine plant nutrient concentrations, it is likely that the effect of drought stress is not uniform across time, space or species.

The implications of drought stress potentially altering or reducing plant nutrient concentrations may not be inconsequential. It may not only affect the health of plants but also the condition and maintenance of herbivores that feed on them (De Bruyn et al. 2002). For herbivores to meet their maintenance, growth and reproduction requirements, a certain degree of nutrient assimilation into the tissue is required (Novellie 1983). Therefore, the performance of herbivores is dependent on the nutritional quality and digestible energy of the forage they ingest (Mbatha and Ward 2006). As such, forage of low nutritive value is often the main cause of reduced animal production (Lukhele 2002). Malnutrition can also affect the fitness of as it increases the risk of disease and predation (Novellie 1983).

Elements of particular importance in herbivore diets and commonly used as indicators of plant nutrition are phosphorus (P), nitrogen (N) (in the form of crude protein), calcium (Ca) and neutral detergent fibre (NDF) concentrations (Skarpe and Bergström 1986; Badri and Hamed

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2000; Lukhele 2000; Scogings et al. 2004; Stapelberg et al. 2008). Plants with high protein concentrations can indicate potentially rapid digestion rates and high nutritional value, not only in terms of the protein available but also the availability of energy and other nutrients (Owen-Smith and Novellie 1982, Novellie 1983). Subsequently, forage with low CP concentrations is often cited as a major limiting factor for sustaining herbivores (Meissner et al. 1999). Phosphorus deficiencies in turn can result in a loss of appetite, a decline in milk production, fragility and the fracturing of bones, low conception rates and failure to come into oestrus (Underwood, 1966). According to McDowell (1996), phosphorus is often the mineral most deficient in natural rangelands. The NDF concentrations of plants, are indicators of plants' cellulose and lignin content and negatively affect fodder intake (Küchenmeister et al. 2013).

For the maintenance of herbivore populations, the potential impact of drought on the nutritive value of natural forage may be as equally important as the associated decreases in availability. More importantly, nutrient-deficient forage, in combination with reduced forage quantities, can be particularly detrimental to herbivore performance and ultimately affect survival rates. Witsand Nature Reserve, located within the southern Kalahari of South Africa, was subjected to the longest and most intense drought recorded in the region in the last 60 years (Chikoore and Jury 2021). The severe drought resulted in herbaceous plant diebacks and high animal mortalities of many herbivore species. This study aimed to determine if the prolonged drought within this semi-arid rangeland resulted in nutrient-deficient plants and contributed to the declines observed in wild herbivore populations. Drought conditions were expected to result in nutrient deficiencies in many plant species and, ultimately, been a contributing factor of herbivore mortalities.

2. Study area

2.1. Locality

The study was conducted on Witsand Nature Reserve (WNR), located 50 km southwest of Postmansburg in the Northern Cape province of South Africa (28º33'08 S and 22º29'10 E). The fenced 3 100 ha reserve lies within the southwestern section of the Eastern Kalahari Bushveld bioregion of the savanna biome (Dayaram et al. 2019).

The area receives summer rainfall, mainly in the form of thunderstorms. The mean annual rainfall of WNR as measured on the Reserve from 1962 to 2022 is 260 mm and highly variable with a coefficient of variation of 44,3% (Figure 1.) Rainfall peaks from January to March, with little to no precipitation during the cold, dry winter months of May to September.

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The Reserve falls mainly within Olifantshoek Plains Thornveld (SVk 13) and very marginally within the Gordonia Plains Shrubland (SVk 16) vegetation types (Dayaram et al. 2019). The vegetation of WNR is particularly diverse for the area, with seven distinct habitat types described (Smit 2018), which include grassland, open woodlands, and sparsely vegetated dune veld.

3. Methodology

3.1. Selection of species and sampling

Twenty woody species (large dicot shrubs and trees) and twenty-one grass species (monocots) were included in the study (Appendix A and B), representing the most abundant plant species on the Reserve and the main forage resource of herbivores. Fifteen individuals per woody species were randomly selected and marked for resampling. Since resampling of individual grasses was not possible, patches of growth were randomly selected instead. Individuals and patches were randomly selected across all habitat types where species occurred. The selection also ensured that plants across a size spectrum were included. Samples were collected monthly during the wet season (W) from January to March, the early dry season (ED) from May to July and the late dry season (LD) from August to October. Sampling was done during the drought in 2020 and the first wet year post-drought in 2021. Woody samples consisted of leaves and the first 30 mm of stems, regarded as the browsable portion of the plant. Several grass tuffs (3-10) within each selected patch were clipped to stubble height (5-10 cm), and the clipped material was collected. In instances of small annual species, all aboveground material was harvested.

3.2 Analyses of nutrient contents

The collected material was oven-dried at 70 C° for 72 hours to a constant mass. The dried material was milled to pass through a 1 mm mesh screen and stored in an airtight container. Monthly samples collected during each season were pooled in equal quantities to form a representative sample of the respective season. The crude protein (CP), Neutral detergent fibre (NDF), and macro nutrients: calcium (Ca), magnesium (Mg) and phosphorus (P) concentrations of all samples were then determined. The standard Kjedahl method (Robbins 1983) was used to determine the percentage of nitrogen in samples. Crude protein was calculated using the simple conversion equation of %N x 6.25 (Robbins 1983). Neutral detergent fibre (NDF) was determined in accordance with the procedure outlined by Van Soest

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et al. (1991). The macro nutrient concentrations (Ca, P, Mg) were determined by means of absorption spectrometry using the AOAC (2012) procedure. The University of the Free States Animal Science lab did all chemical analyses. The results of all species analyses are included in Appendix A and B.

3.3. Statistical analyses

The distribution of all data was established by plotting and visually inspecting QQ plots and validated by means of the Shapiro- Wilks test. In instances of non-normal distributed data, a log transformation was performed. Significant differences in mean nutrient concentrations between sampling seasons (W vs ED vs LD) and years (drought year vs wet year) were determined for woody and herbaceous species, respectively. For the comparisons of mean seasonal nutrient content within the same year of sampling (E.g., W vs ED vs LD in 2020), repeated measure analyses of variance (ANOVA) analyses were conducted. Depending on the GG epsilon value of the analyses, either the Greenhouse-Geisser (GG epsilon < 0.75) or Huynh and Feldt (GG epsilon > 0.75) correction factor was applied. Tukeys HDS *post-hoc* was conducted to determine where significant differences occurred. Comparisons of seasonal nutrient values between sampling years (e.g., W during drought vs W after drought, etc.) were done by means of the *t*-test for two paired samples.

4. Results

4.1. CP concentrations

Drought stress (2020 vs 2021) resulted in substantially higher mean CP concentrations in grasses (2020: W = 8.7%, ED = 5.1%, LD = 4.2% vs 2021: W = 5.0%, ED = 3.8%, LD = 3.2%), but marginally lower CP concentrations in woody plants (2020: W = 15.7%, ED = 14.3%, LD = 14.3% vs 2021: W = 16%, ED = 13.5%, LD = 16.3%). This trend was observed in all grass species studied, while four of the 20 woody species had slightly elevated CP consecrations during the drought. The CP concentration of woody species was typically higher compared to those of grasses. CP declined from the wet to late dry season where declines were greater in grasses (Figure 1.).

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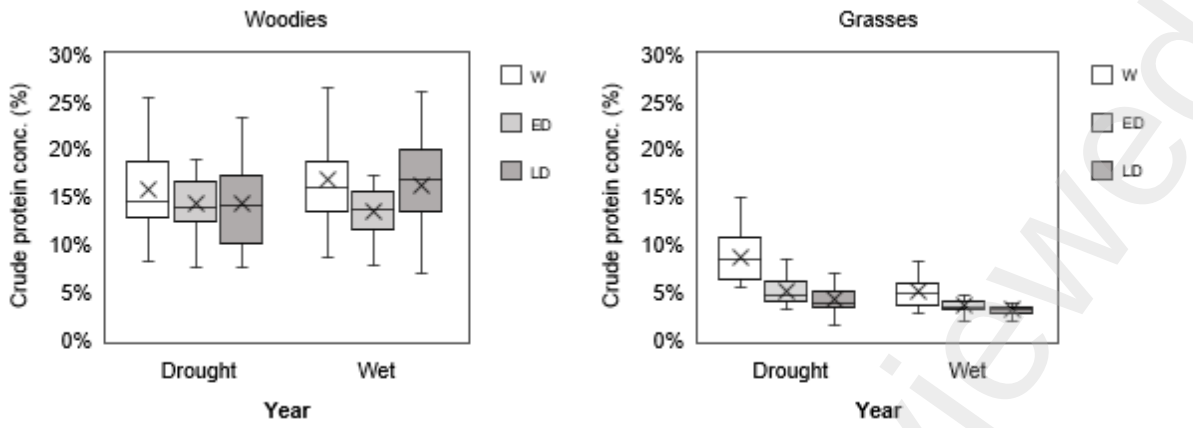


Figure 1. The mean CP concentrations of plants in the wet (W), early dry (ED) and late dry season (LD), both in the drought and wet year

During the drought, the mean CP of woody species remained similar between seasons ($F_{1.3, 24.5}$ = 1,89, p = 0.18) but varied significantly ($F_{2, 37.9}$ = 10.5, p < 0,001) during the wet year. In the wet year, significant differences were between the W and ED and the ED and LD (Table 1). The similar CP concentrations of the W and LD could be attributed to the early start of the wet season in 2021, which resulted in many species flushing new leaves. Seasonal CP concentrations of grasses were found to differ significantly during the drought year ($F_{1.8, 35.9}$ = 73.5, p < 0,001) and wet year ($F_{1.7, 34.8}$ = 22.8, p = 0,001) (Figure). The CP differed significantly between all seasons during drought, while post-drought significant differences were between the W and ED and W and LD, respectively (Table 1).

Table 1. Analyses of seasonal CP concentrations of each sampling year. Means differed significantly (p < 0.05) between the W, ED and LD in drought and wet years, respectively. Results include the post-hoc where repeated measure ANOVA was insignificant (p > 0.05) for reference purposes.

Drought year					Wet year				
Season	Mean diff	q	p	Cohen's d	Season	Mean diff	q	p	Cohen's d
Woodies									
W vs. ED	1.37	2.35	0.23	0.53	W vs. ED	3.40	6.13	< 0.001	1.37
W vs. LD	1.41	2.41	0.22	0.54	W vs. LD	0.65	1.18	0.690	0.26
ED vs. LD	0.03	0.06	1.00	0.01	ED vs. LD	2.75	4.95	0.003	1.11
Grasses									
W vs. ED	3.57	11.94	< 0.001	2.60	W vs. ED	1.27	6.16	< 0.001	1.34
W vs. LD	4.43	16.63	< 0.001	3.63	W vs. LD	1.80	9.41	< 0.001	2.05
ED vs. LD	0.86	4.70	0.005	1.03	ED vs. LD	0.53	3.25	0.070	0.71

W = wet season (Jan- Mar), ED = early dry season (May – Jul), LD = late dry season (Aug - Oct)

Results of the paired *t*-test found that mean CP concentrations of both woody and grass species differed significantly (p < 0.05) between the drought and wet years for all seasons tested (Table 2). Specifically, the mean W and LD crude protein content of woody species was

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lower during the drought, while in the ED, it was higher. In contrast, the mean CP content of grasses was higher throughout the drought year than the wet year. Test results also indicated that the drought strongly affected CP concentrations, except for CP of woody species during the ED (Table 2).

Table 2. Comparison of mean season CP concentrations of plants between sampling years (drought year vs wet year) for significant differences ($p < 0.05$).

Seasons	Mean diff	t	p	Cohen's d
Woodies				
W	1.25	-3.35	0.008	0.65
ED	0.77	-3.32	0.045	0.48
LD	2.00	-4.55	< 0.001	1.16
Grasses				
W	3.64	11.79	< 0.001	2.57
ED	1.34	5.18	< 0.001	1.13
LD	1.01	3.45	0.002	0.75

W = wet season (Jan- Mar) of 2020 vs wet season of 2021
ED = early dry season (May – Jul) of 2020 vs wet season of 2021
LD = late dry season (Aug - Oct) of 2020 vs wet season of 2021

4.2. NDF Concentrations

The seasonal NDF concentrations of woodies remained similar during and after the drought (2020: W = 41.3%, ED = 38.9%, LD = 40.8% vs 2021: W = 44.2%, ED = 41.2%, LD = 40.3%), as indicated in Figure 4. Despite the similarities in NDF, seasonal mean differences were still statistically significant for the drought year ($F_{2, 38} = 6.59$, $p = 0.003$) and wet year ($F_{1.6, 31.6} = 7.20$, $p = 0.004$). Significant differences ($p < 0.05$) occurred during the drought between the W and ED and ED and LD. After the drought, it was between the W and ED and W and LD (Table 3). The NDF of grasses were typically much higher compared to woody species. Grasses also did not fluctuate greatly between seasons in both the drought and wet year (2020: W = 74.2%, ED = 76.6%, LD = 72.2% vs 2021: W = 79.2%, ED = 79.4%, LD = 77.4%) (Table 3.). Changes in seasonal means were also significant ($p < 0.05$) for both the drought and wet years, respectively.

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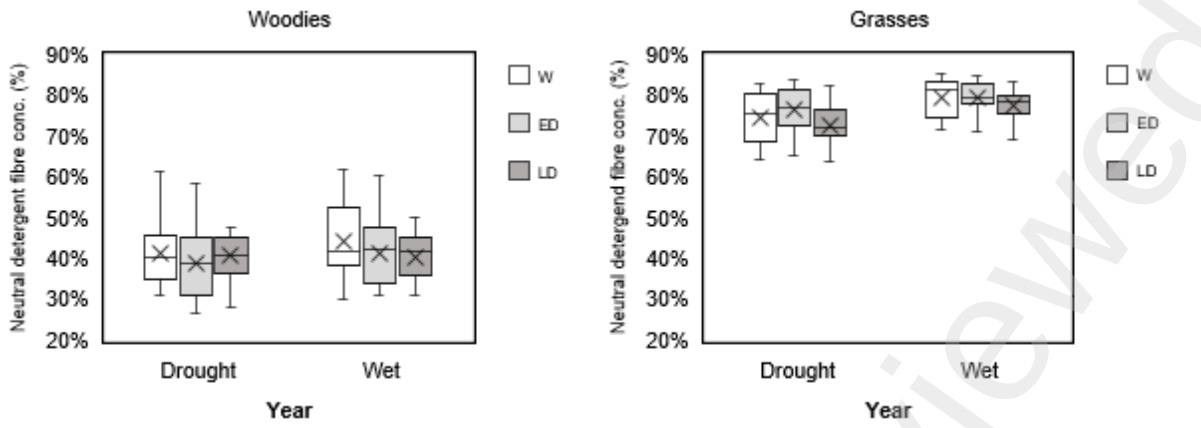


Figure 2. The mean NDF concentrations of plants in the wet (W), early dry (ED) and late dry season (LD), Both in the drought and wet year.

Table 3. Analyses of season NDF concentrations within each sampling year. Means differed significantly ($p < 0.05$) between the W, ED and LD in drought and wet years, respectively. Results include the post-hoc where repeated measure ANOVA was insignificant ($p > 0.05$) for reference purposes.

	Drought year					Wet year			
Season	**Mean diff**	**q**	**p**	**Cohen's d**	**Season**	**Mean diff**	**q**	**p**	**Cohen's d**
				Woodies					
W vs. ED	2.46	4.91	0.004	1.10	W vs. ED	3.05	3.98	0.020	0.89
W vs. LD	0.57	1.14	0.700	0.25	W vs. LD	3.92	5.11	0.002	1.14
ED vs. LD	1.89	3.77	0.030	0.84	ED vs. LD	0.86	1.13	0.700	0.25
				Grasses					
W vs. ED	2.39	4.14	0.015	0.91	W vs. ED	0.14	0.35	0.970	0.08
W vs. LD	1.75	3.04	0.092	0.66	W vs. LD	1.87	4.73	0.005	1.03
ED vs. LD	4.14	7.19	<0.001	1.57	ED vs. LD	2.01	5.09	0.002	1.11

W = wet season (Jan- Mar), ED = early dry season (May – Jul), LD = late dry season (Aug - Oct)

The comparison of NDF concentrations of woodies and grasses revealed that season NDF were significantly ($p < 0.05$) lower during the drought compared to after, except for woody species during the LD season (Table 4).

Table 4. Comparison of mean season NDF concentrations of plants between sampling years (Drought year vs wet year) for significant differences ($p < 0.05$).

Seasons	Mean diff	t	p	Cohen's d
Woodies				
W	2.88	-3.20	0.005	0.71
ED	2.30	-3.32	0.004	0.74
LD	0.46	-0.51	0.617	0.11
Grasses				
W	5.07	-7.62	< 0.001	1.66
ED	2.82	-3.39	0.003	0.74
LD	4.94	-6.57	< 0.001	0.81

W = wet season (Jan- Mar) of 2020 vs wet season of 2021
ED = early dry season (May – Jul) of 2020 vs wet season of 2021
LD = late dry season (Aug - Oct) of 2020 vs wet season of 2021

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4.3. Macronutrients

The concentration of all tested macronutrients in woody species was higher during the drought than after the drought. The concentration of Ca and Mg in grasses was also higher during the drought, but P was substantially lower (Figure 3).

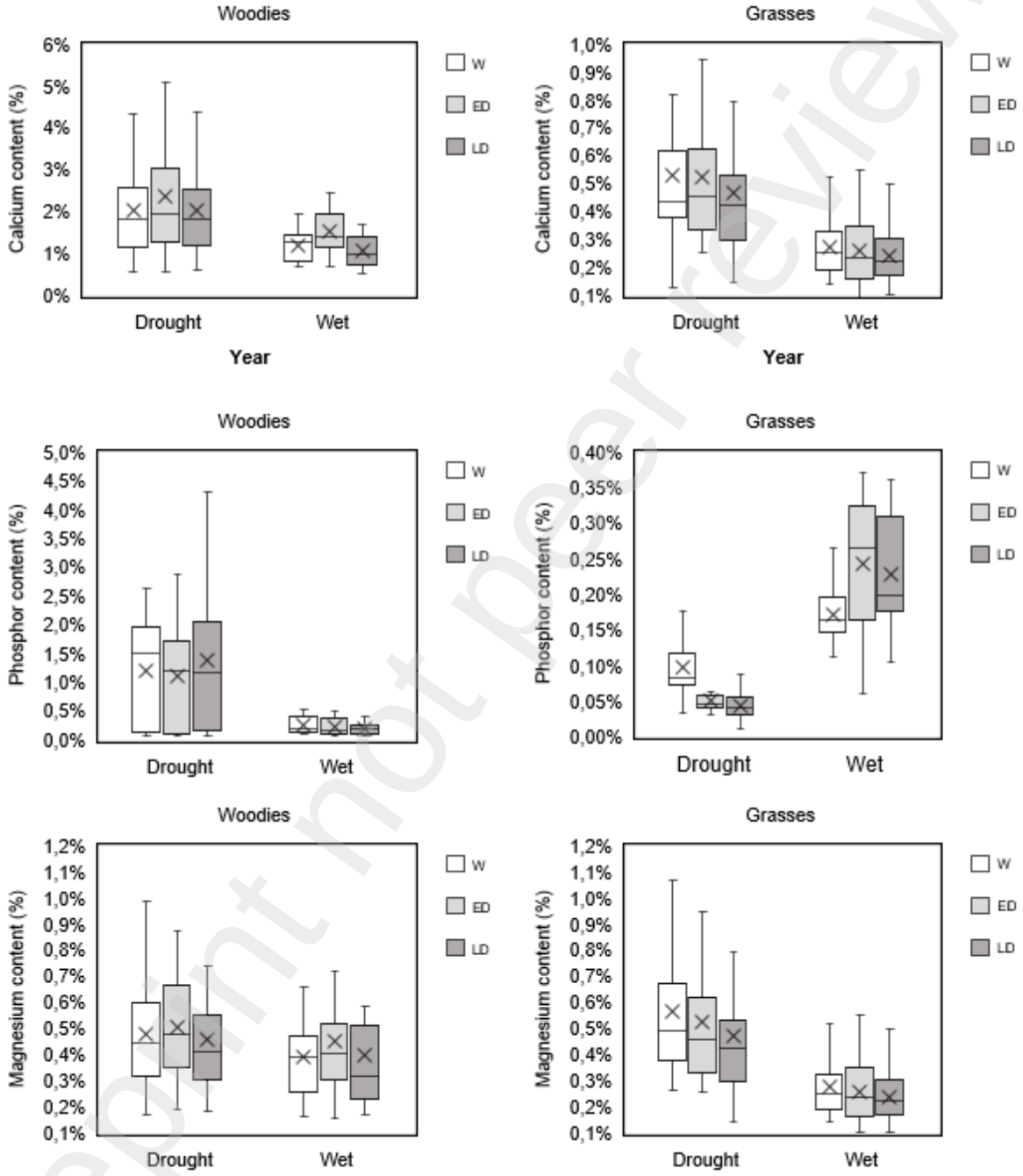


Figure 3. The mean macronutrient concentrations of plants in the wet (W), early dry (ED) and late dry season (LD), Both in the drought and wet year.

Seasonal differences in Ca and Mg concentrations of woody species were negligible ($p > 0.05$) during the drought but significant for P ($p < 0.05$). All macronutrients differed significantly ($p <$

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0.05) post drought, where differences were Ca: W vs ED and ED vs LD, Mg: W vs ED and W vs LD, P: W vs LD and LD vs ED (Table 5).

Table 5. Season macronutrient (Ca, MG, P) concentrations are analysed within each sampling year. Means differed significantly ($p < 0.05$) between the W, ED and LD in drought and wet years, respectively. Results include the post-hoc where repeated measure ANOVA was insignificant ($p > 0.05$) for reference purposes.

	Drought year					Wet year			
Season	Mean diff	q	p	Cohen's d	Season	Mean diff	q	p	Cohen's d
Ca woodies									
W vs. ED	0.36	2.17	0.285	0.47	W vs. ED	0.36	4.65	0.006	1.04
W vs. LD	0.02	0.14	0.994	0.03	W vs. LD	0.13	1.70	0.460	0.38
ED vs. LD	0.33	2.03	0.334	0.45	ED vs. LD	0.49	6.34	<0.001	1.42
Ca grasses									
W vs. ED	0.04	0.09	0.998	0.02	W vs. ED	0.02	2.23	0.270	0.50
W vs. LD	0.06	2.29	0.250	0.50	W vs. LD	0.04	2.83	0.125	0.63
ED vs. LD	0.06	2.38	0.225	0.52	ED vs. LD	0.02	0.60	0.905	0.14
Mg woodies									
W vs. ED	0.03	1.65	0.480	0.37	W vs. ED	0.06	3.98	0.020	0.89
W vs. LD	0.02	0.89	0.807	0.20	W vs. LD	0.004	5.11	0.002	1.14
ED vs. LD	0.05	2.53	0.186	0.57	ED vs. LD	0.06	1.13	0.700	0.25
MG grasses									
W vs. ED	0.06	3.89	0.020	0.86	W vs. ED	0.01	1.08	0.726	0.24
W vs. LD	0.13	7.90	<0.001	1.76	W vs. LD	0.02	1.86	0.396	0.41
ED vs. LD	0.07	4.02	0.020	0.90	ED vs. LD	0.02	2.94	0.107	0.64
P woodies									
W vs. ED	0.1	0.90	0.800	0.20	W vs. ED	0.02	1.38	0.570	0.31
W vs. LD	0.2	6.39	< 0.001	1.42	W vs. LD	0.06	14.2	< 0.001	3.19
ED vs. LD	0.3	7.30	< 0.001	1.63	ED vs. LD	0.03	15.64	< 0.001	3.50
P grasses									
W vs. ED	0.05	8.84	< 0.001	1.92	W vs. ED	0.08	7.08	< 0.001	1.54
W vs. LD	0.05	11.48	< 0.001	2.50	W vs. LD	0.06	5.60	0.001	1.22
ED vs. LD	0.01	2.64	0.160	0.58	ED vs. LD	0.02	1.48	0.055	0.32

Ca = Calcium, Mg = Magnesium, P = Phosphor

W = wet season (Jan- Mar), ED = early dry season (May – Jul), LD = late dry season (Aug - Oct)

Calcium and Magnesium concentrations in woodies and grasses were significantly higher ($p < 0.05$) in the drought year, except for ED and LD concentrations of Mg in woody species. The effect of drought on P concentrations was the opposite for woodies and grasses. In woody species, P concentrations were significantly higher ($p < 0.05$) in the drought year, while for grasses, it was significantly ($p > 0.05$) lower (Table 6).

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Table 6. Comparison of mean season macronutrient concentrations of plants between sampling years (drought year vs wet year) for significant differences ($p < 0.05$).

	Woodies					Grasses			
Season	Mean diff	t	p	Cohen's d	Season	Mean diff	t	p	Cohen's d
Ca					***Ca***				
W	0.84	3.80	< 0.001	0.85	W	0.25	8.80	< 0.001	1.94
ED	0.84	3.03	0.006	0.67	ED	0.26	8.09	< 0.001	1.77
LD	1.00	4.13	0.001	0.92	LD	0.22	6.97	< 0.001	1.52
Mg					***Mg***				
W	0.08	2.20	0.036	0.50	W	0.14	5.49	< 0.001	1.20
ED	0.05	1.27	0.220	0.28	ED	0.07	6.45	< 0.001	1.41
LD	0.06	2.10	0.05	0.47	LD	0.03	2.23	0.037	0.49
P					***P***				
W	0.95	4.28	< 0.001	0.96	W	0.07	-6.87	< 0.001	1.50
ED	0.87	4.42	< 0.001	0.99	ED	0.20	-14.59	< 0.001	3.18
LD	1.20	4.12	0.001	0.92	LD	0.19	-12.49	< 0.001	2.73

Ca = Calcium,
Mg = Magnesium
P = Phosphor
W = wet season (Jan- Mar) of 2020 vs wet season of 2021
ED = early dry season (May – Jul) of 2020 vs wet season of 2021
LD = late dry season (Aug - Oct) of 2020 vs wet season of 2021

5. Discussion

It was evident that the effect of drought on the nutrient status of plants differed markedly between grasses (monocotyledons) and woody plants (dicotyledons). In most woody species (80%), drought stress resulted in lower CP concentrations but higher NDF and macro nutrient concentrations. The CP, Ca and Mg concentrations were higher during the drought in all studied grasses, and NDF and P were lower. These results were in many aspects contradicting to the literature, which generally concluded that drought stress reduced plant nutrients (e.g. Peterson et al. 1992; Schimel et al. 2007; Cramer et al. 2009; Lashy and Harper 2012; Küchenmeister et al. 2013; He and Dijkstra, 2014; Bista et al. 2020). The higher CP concentrations and lower NDF concentrations of woody plants compared to grasses were expected. It is well known that the non-woody parts of dicots, like the leaf and shoots, have higher CP concentrations than grasses (Boutton et al. 1988; Lukhele 2002; Codron et al. 2007). These parts of dicots also have greater quantities of cell-soluble compounds than grasses, while the amount of structural carbohydrates and lignin is also lower. However, the relatively higher nutritive value of woodies is limited by secondary compounds, like tannins and alkaloids, which often inhibit microbial fermentation (Hegarty 1982; Stapelberg et al. 2008).

Wet and dry seasons naturally create a cycle of alternating food abundance and quality. Seasonal differences in plant nutrients in the semi-arid Kalahari is especially wide (e.g. Skarpe

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and Bergström 1986; Stabelberg 2008). In the Kalahari, the nutrient concentrations of grasses rapidly increase with the onset of spring and peak when grasses are in flower during the hot and wet summer months. As grasses mature towards autumn, nutrients decline (Stapelberg et al. 2008). Generally, the degree of seasonal fluctuations in the nutrient concentration of woody species is less than that of grasses (Lukhele 2002). Surprisingly, Stabelberg et al. (2008) found that the nutrient concentration of woody species in the Kalahari Gemsboks Park fluctuated as greatly as grasses, if not more so. In this study, seasonal changes in nutrient concentrations of woody species were far more gradual than those of grasses. Importantly, the drought did not alter the general pattern of seasonal nutrient changes of woody or grass species. The higher nutrient concentrations also highlighted the importance of woody plants as an alternative fodder source during dry months.

The protein requirements of wild ruminants typically range between 5-9% of their diet (Holter et al. 1979). McDowell (2003) specified that 6% CP concentration is the critical threshold to maintain ruminants. Similarly, Van Hoven (2002) stated that the diet of African ruminants must contain a crude protein concentration of at least 5%. Most ruminants need at least 0.18% Ca and P and 0.20% Mg of the dry matter mass eaten for maintenance (McDowell 1997, 2003). The CP concentration of most grasses in the late dry season, both in the drought and wet year, were below the cited critical levels required to maintain ruminants. In the drought year, only five of the 20 grass species had greater CP concentrations of 5%. In the wet year, only a single species was above the threshold (Table 7). Despite the significant decreases in CP concentration in the drought year of woody plants, the concentrations remained well above the critical threshold. Phosphorus was found to be the most limiting nutrient in the study area. Almost all grass species were P deficient throughout the drought year, but P levels increased during the wet year.

In comparison, roughly a third of woody species were P deficient in the drought year and about half of all species in the wet year (Table 7). Phosphor deficiencies in plants are a common occurrence in South Africa (Boyazoglu 1997) and have been reported to be deficient in the Kalahari region as well (Skarpe and Bergström 1986; Stapelberg et al. 2008). Calcium was the least limiting nutrient throughout the study period, as only a few grass species had Ca consecrations below the critical threshold. Magnesium was far more limiting in grasses than woody species during both the drought and wet year. Levels of Mg were elevated during the drought. As a result, the Mg concentrations of most species were above the critical threshold, while in the wet year, only a handful had Mg concentrations above the threshold. The actual diet quality of herbivores, particularly of grazer species, was probably greater than what the level of plant nutrients in this study suggested. This is because ungulates can select the most

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nutrient-rich parts of the plant or be selective of the species they graze (Dziba et al. 2003, Mbatha and Ward 2006). Also, not all plant species were available to herbivores, and fewer were included in the study.

Table 7. The number of plant species that were found to have had nutrient concentrations below (<) or equal or above (≥) the critical threshold levels required for sustaining ruminants over the study period.

	Drought year								Wet year							
	CP		Ca		Mg		P		CP		Ca		MG		P	
	<	≥	<	≥	<	≥	<	≥	<	≥	<	≥	<	≥	<	≥
Woody species (n =20)																
W	0	20	0	20	1	19	6	14	0	20	0	20	2	18	10	10
ED	0	20	0	20	2	18	7	13	0	20	0	20	1	19	11	9
LD	0	20	0	20	1	19	7	13	0	20	0	20	2	18	8	12
Grass species (n = 21)																
W	0	21	1	20	8	13	17	4	12	9	2	19	17	4	16	5
ED	13	8	0	21	13	8	21	0	18	3	5	16	15	6	5	16
LD	16	5	2	19	15	6	21	0	20	1	4	17	17	4	4	17

Thresholds: CP = 5%, Ca = 0.18%, Mg = 0.2%, P = 0. 18 %

The results indicated that the nutritional value of the forage during the drought, apart from P deficiencies in grasses, was not a limiting factor for herbivores on WNR. Grasses and some woody species were found to be even more nutritious during the drought. The amount of herbage and browse available to herbivores was far more restrictive. The drought, however, greatly prolonged the critical period of the year (i.e. late dry season) when the nutritional value of plants was naturally at their lowest. In the southern Kalahari, the first rainfall of the growing season usually falls in October or November. During the drought, the season's first rainfall was often only received by late January or early February. It was usually not sufficient to stimulate new growth in all species.

Many herbivore species adapted to semi-arid environments can overcome dry season food limitations by increasing daily food intake (Owen-Smith and Cooper 1985; Dekker and Smit 1996). Several plant species may also be crucial supplementary feed species for herbivores that help bridge the critical dry season (Owen-Smith and Cooper 1985; Buys 1990). Furthermore, herbivores depend on body fat reserves built up over the growing season to help overcome the resource limitations of the dry seasons (Fryxell 1987). However, during the drought, food quantities are even more limiting and key species may not be as readily available. The drought's shortened growing season (wet season) may also have restricted the build-up of fat reserves. The subsequently lower fat reserves at the start of the dry season, combined with its greatly extended duration, was probably the main driver of the herbivore mortalities observed.

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6. Conclusion

The impact of drought stress on plant nutrient concentrations was not constant between dicots and monocots, often conflicting with the available literature. The reasons for observed differences were, however, not studied. Plants ' physiological adaptations and differing responses to drought stress may likely be species-specific traits and region- and climate-dependent. However, this study found that the severe drought affected the nutritional concentrations of all plants on WNR in some form or another. Importantly, the drought did not result in nutrient-deficient fodder and, therefore, did not impact the performance and maintenance of herbivores on the Reserve. It was concluded that forage availability, both browse (woody plants) and herbage (grasses), during the drought years was a bigger constraining factor in sustaining WNR's herbivore population. The drought did, however, alter wet and dry cycle durations. The drought extended the persistence of the dry season and, as a result, shortened the active growing wet season. The consequences were an unbalanced cycle of low food quantity and quality during the dry season and high quantity and quality during the wet season. It was ultimately concluded that the extended dry period was too long for many herbivores to overcome and the main driver of herbivore mortalities observed on WNR. Many landowners provide additional feed to overcome dry periods and droughts. This study provided evidence that the feed provided may not need to supplement any nutrient deficiencies. This may, however, be area and species-dependent.

References

AOAC (Association of Official Analytical Chemists). 2012. Official methods of analysis, nineteenth ed. AOAC, Arlington.

Badri, M.A., Hamed, A.I. 2000. Nutrient value of plants in an extremely arid environment (Wadi Allaqi Biosphere Reserve, Egypt). Journal of Arid Environments. 44, 347–356. https://doi.org/10.1006/jare.1999.0585.

Bista, D.R., Heckathorn, S.A., Jayawardena, D.M., Boldt, J.K. 2020. Effect of drought and carbon dioxide on nutrient uptake and levels of nutrient-uptake proteins in roots of barley. American Journal of Botany. 107(10), 1401–1409. https://doi.org/10.1002/ajb2.1542.

Preprint not peer reviewed

This preprint research paper has not been peer reviewed. Electronic copy available at: https://ssrn.com/abstract=4666298

Bodner, G.S., Robles, M.D. 2017. Enduring a decade of drought: Patterns and drivers of vegetation change in a semi-arid grassland. Journal of Arid Environments. 136, 1–14. https://doi.org/10.1016/j.jaridenv.2016.09.002.

Boutton, T.W., Tieszen, L.L., Imbamba, S.K. 1988. Seasonal changes in the nutrient content of East African grassland vegetation. African Journal of Ecology. 26,103-105. https://doi.org/10.1111/j.1365-2028.1988.tb00961.x.

Boyazoglu, P.A. 1997. Animal Nutrition: Concepts and Application. Van Schaik, Pretoria, South Africa.

Buys, D. 1990. Food selection by eland in the western Transvaal. South African Journal of Wildlife Research. 20(1), 16-20.

Chikoore, H., Jury, M.R. 2021. South African drought, deconstructed. Weather and Climate Extremes. 33. https://doi.org/10.1016/j.wace.2021.100334.

Codron, D., Lee-Thorp, J.A., Sponheimer, M. Codron, J. 2007. Nutritional content of savanna plant foods: implications for browser/grazer models of ungulate diversification. European Journal of Wildlife Research. 53, 100- 111. https://doi.org/10.1007/s10344-006-0071-1.

Cramer, M.D, Hawkins, H.J., Verboom, G.A. 2009. The importance of nutritional regulation of plant water flux. Oecologia. 161, 15–24. https://doi.org/10.1007/s00442-009-1364-3.

Dayaram, A., Harris, L.R., Grobler, B.A. Van der Merwe, S., Ward Powrie, L., Rebelo, A.G. 2019. Vegetation Map of South Africa, Lesotho and Swaziland 2018: A description of changes since 2006. Bothalia. 49(1), a2452. https://doi.org/10.4102/ abc.v49i1.2452.

De Bruyn, L., Scheirs, J., Verhagen, R. 2002. Nutrient Stress, Host Plant Quality and Herbivore Performance of a Leaf-Mining Fly on Grass. Oecologia. 130(4), 594–599. https://doi.org/10.1007/s00442-001-0840-1.

Dekker, B., Smit, G.N. 1996. Browse production and leaf phenology of some trees and shrubs in different *Colophospermum mopane* savanna communities. African Journal of Range and Forage Science. 13(1), 15-23. https://doi.org/10.1080/10220119.1996.9647888.

Preprint not peer reviewed

This preprint research paper has not been peer reviewed. Electronic copy available at: https://ssrn.com/abstract=4666298

Dziba, E.L., Scogings, P.F., Gordon, I.J., Raats J.G. 2003. Effects of season and breed on browse species intake rates and diet selection by goats in the False Thornveld of the Eastern Cape, South Africa. Small Ruminant Research. 47,17–30. https://doi.org/10.1016/s0921-4488(02)00235-3.

Fierer, N., Schimel, J.P. 2002. Effects of drying–rewetting frequency on soil carbon and nitrogen transformations. Soil Biology & Biochemistry. 34, 777–787. https://doi.org/10.1016/s0038-0717(02)00007-x.

Fryxell, J.M. 1987. Food limitation and demography of a migratory antelope, the white-eared kob. Oecologia. 72, 83–91. https://doi.org/10.1007/BF00385049.

He, M., Dijkstra, F.A. 2014. Drought effect on plant nitrogen and phosphorus: a meta-analysis. New Phytologist. 204,924-931. https://doi.org/10.1111/nph.12952.

Hegarty, M.P. 1982. Deleterious factors in forages affecting animal production, in: Hacker J.B. (Ed.), Nutritional limits to animal production from pastures. Commonwealth Agricultural Bureaux, Farnham Royal UK, pp. 133-150.

Holter, J.B., Hayes, H.H., Smith, S.H. 1979. Protein requirement of yearling white-tailed deer. The Journal of Wildlife Management. 43(4), 872–879. https://doi.org/10.2307/3808270.

Knapp, A.K., Ciais, P., Smith, M.D. 2017. Reconciling inconsistencies in precipitation–productivity relationships: implications for climate change. New Phytologist. 214(1), 41–47. https://doi.org/10.1111/nph.14381.

Küchenmeister, K., Küchenmeister, F., Kayser, M., Wrage-Mönnig, N., Isselstein, J. 2013. Influence of drought stress on nutritive value of perennial forage legumes. International Journal of Plant Production. 7, 1735-6814.

Kumar, D., Singh, M., Kushwaha, M. 2021. Nutrient content, uptake and NUE of oats (2). Indian Journal of Agronomy. 66. 466-473.

Preprint not peer reviewed

This preprint research paper has not been peer reviewed. Electronic copy available at: https://ssrn.com/abstract=4666298

Lashley, M.A., Harper, C.A. 2012. The effects of extreme drought on native forage nutritional quality and white-tailed deer diet selection. Southeastern Naturalist. 11(4), 699–710. https://doi.org/10.1656/058.011.0409.

Lukhele, M.S. 2002. The chemical composition and nutritive value of leaves of indigenous fodder trees. MSc dissertation, University of Pretoria, Pretoria, South Africa. http://hdl.handle.net/2263/27265.

Mbatha, K.R., Ward, D. 2006. Determining spatial and temporal variability in quantity and quality of vegetation for estimating the predictable sustainable stocking rate in the semi-arid savanna. African Journal of Range and Forage Science. 23(2), 131–145. https://doi.org/10.2989/10220110609485896.

McDowell, L.R. 1996. Feeding minerals to cattle on pasture. Animal Feed Science and Technology. 60, 247–271. https://doi.org/10.1016/0377-8401(96)00983-2.

McDowell, L.R. 1997. Minerals for Grazing Ruminants in Tropical Regions, third ed. University of Florida, Gainsville, Florida, USA.

McDowell, L.R. 2003. Minerals in animal and human nutrition, second ed. Amsterdam: Elsevier.

Meissner, H.H., Zacharias, P.J.K., O'Reagain, P.J. 1999. Forage quality (feed value), in: Tainton, N.M. (Ed.) Veld management in South Africa. University of Natal Press, Pietermaritzburg, South Africa, pp139–168.

Milton, S.J., Petersen, H., Nampa, G., Van der Merwe, H., Henschel, J.R. 2023. Drought as a driver of vegetation change in Succulent Karoo rangelands, South Africa. African Journal of Range & Forage Science. 40(2), 181-195. https://doi.org/10.2989/10220119.2021.1992501.

Preprint not peer reviewed

This preprint research paper has not been peer reviewed. Electronic copy available at: https://ssrn.com/abstract=4666298

Novellie, P. 1983. Feeding ecology of the kudu *Tragelaphus strepsiceros* (Pallas) in the Kruger National Park. Unpublished D.Sc. thesis, University of Pretoria, Pretoria. https://repository.up.ac.za/handle/2263/85362.

Owen-Smith, N. 1979. Assessing the foraging efficiency of a large herbivore, the kudu. South African Journal of Wildlife Research 9(3/4), 102-110.

Owen-Smith, N., Cooper, S.M. 1985. Comparative consumption of vegetation components by kudus, impalas and goats in relation to their commercial potential as browsers in savanna regions. South African Journal of Science, 81: 72-76.

Owen-Smith, N., Novellie, P. 1982. What should a clever ungulate eat? American Naturalist. 119(2), 151-178. https://doi.org/10.1086/283902.

Peterson, P.R., Sheaffer, C.C., Hall, M.H. 1992. drought effects on perennial forage legume yield and quality. Agronomy Journal. 84, 774-779. https://doi.org/10.2134/agronj1992.00021962008400050003x.

Robbins, C.T. 1993. Wildlife feeding and nutrition, second ed. Academic Press, New York.

Sanaullah, M., Rumpel, C., Charrier, X., Chabbi, A. 2012. How does drought stress influence the decomposition of plant litter with contrasting quality in a grassland ecosystem? Plant and Soil. 352, 277–288. https://doi.org/10.1007/s11104-011-0995-4.

Schimel, J., Balser, T.C., Wallenstein, M. 2007. Microbial stress-response physiology and its implications for ecosystem function. Ecology. 88, 1386–1394.

Scogings, P.F., Dziba, L.E., Gordon, I.J. 2004. Leaf chemistry of woody plants in relation to season, canopy retention and goat browsing in a semi-arid subtropical savanna. Austral Ecology 29: 278–286. https://doi.org/10.1111/j.1442-9993.2004.01347.x.

Skarpe, C., Bergström, R. 1986. Nutrient content and digestibility of forage plants in relation to plant phenology and rainfall in the Kalahari, Botswana. Journal of Arid Environments. 11,147-164. https://doi.org/10.1016/s0140-1963(18)31226-6.

Preprint not peer reviewed

This preprint research paper has not been peer reviewed. Electronic copy available at: https://ssrn.com/abstract=4666298

Smit, G.N. 2007. Applied game ranch planning. Unpublished document, Department of Animal, Wildlife and Grassland Sciences, University of the Free State, Bloemfontein.

Smit, Z.M. 2018. Veld condition and carrying capacity assessments of Witsand Nature Reserve 2018. Internal report no: 2/2018. Northern Cape Department of Environment and Nature Conservation, Kimberley.

Stapelberg, F.H., Van Rooyen, M.W., Bothma, J. du P. 2008. Seasonal nutrient fluctuation in selected plant species in the Kalahari. African Journal of Range & Forage Science. 25(3), 111-119. https://doi.org/10.2989/ajrf.2008.25.3.3.600.

Underwood, E.J., Suttle, N.F. 1999. The mineral nutrition of livestock, third ed. CAB International, Wallingford.

Underwood, E.J. 1966. The mineral nutrition of livestock. Aberdeen, Commonwealth Agricultural Bureaux.

Van Hoven, W. 2002. Nutrition. In: Bothma J. du P. (Ed.), Game Ranch Management, fourth ed. Van Schaik Publishers, Pretoria, South Africa, pp 243–276.

Van Soest, P.V., Robertson, J.B., Lewis, B.A. 1991. Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. Journal of Dairy Science. 74(10), pp.3583-3597. https://doi.org/10.3168/jds.s0022-0302(91)78551-2

Waraich, E.A., Ahmad, R., Saifullah, Ashraf, M.Y., Ehsanullah. 2011. Role of mineral nutrition in alleviation of drought stress in plants. Australian Journal of Crop Science. 5, 764-777.

Preprint not peer reviewed

This preprint research paper has not been peer reviewed. Electronic copy available at: https://ssrn.com/abstract=4666298

Appendix A. The concentration of all elements in woody species studies, starting with the wet season concentrations (top value), early wet season (mid value) and late dry season concentration (bottom value).

Species	During drought					After drought				
	CP	NDF	C	Mg	P	CP	NDF	C	Mg	P
Boscia albitrunca	20,2	42,0	1,31	0,94	0,08	26,4	40,3	0,68	0,66	0,15
	17,4	43,7	1,20	0,88	0,07	17,3	44,2	1,20	1,33	0,10
	15,0	40,8	1,54	1,10	0,06	17,0	38,9	1,23	1,27	0,10
Croton gratissimus	17,9	40,8	0,61	0,17	0,18	19,0	45,9	0,89	0,39	0,17
	14,1	38,5	0,68	0,19	0,11	14,9	43,1	1,14	0,43	0,13
	15,8	39,7	0,59	0,18	0,20	18,2	42,5	0,82	0,30	0,18
Diospyros lycioides	11,5	34,3	0,96	0,44	0,10	13,3	38,3	1,48	0,53	0,14
	8,9	29,6	1,15	0,39	0,09	9,1	35,1	1,57	0,63	0,08
	12,4	38,5	0,99	0,37	0,13	13,8	41,6	0,78	0,37	0,21
Ehrethia alba	19,0	30,9	1,03	0,49	0,12	16,3	36,3	1,44	0,48	0,10
	17,0	26,3	1,22	0,49	0,09	16,0	33,2	2,45	0,52	0,11
	17,4	28,2	1,16	0,50	0,15	20,1	30,7	1,31	0,50	0,25
Euclea undulata	8,2	37,1	0,53	0,43	0,10	8,7	51,3	0,67	0,44	0,10
	7,6	42,4	0,54	0,47	0,08	7,7	48,6	0,68	0,52	0,07
	7,5	41,7	0,61	0,41	0,07	6,9	45,6	1,00	0,51	0,07
Grewia flawa	18,0	46,2	1,30	0,32	0,17	17,7	53,0	1,42	0,41	0,17
	13,9	45,9	2,00	0,37	0,11	11,8	44,7	2,05	0,44	0,10
	17,3	44,5	0,67	0,30	0,16	19,8	45,9	1,21	0,35	0,20
Lycium bosciifolium	8,3	33,2	2,41	0,32	0,06	10,0	41,3	1,34	0,44	0,08
	9,0	30,9	2,51	0,39	0,07	8,8	32,4	1,62	0,43	0,09
	7,9	32,3	2,49	0,32	0,05	9,1	30,7	1,68	0,42	0,09
Lycium hirsutum	25,4	35,1	2,63	0,99	0,19	28,7	30,1	1,33	0,95	0,20
	25,3	28,9	2,01	0,87	0,22	21,5	31,2	0,93	0,72	0,25
	17,1	31,5	1,68	0,74	0,16	20,2	36,9	0,70	0,58	0,23
Rhigozum obovatum	13,0	42,7	1,78	0,24	2,50	15,8	41,5	0,77	0,18	0,16
	14,1	34,8	1,68	0,34	2,61	11,6	41,1	0,84	0,15	0,12
	10,9	44,0	2,00	0,27	2,41	13,6	41,7	0,63	0,18	0,19
Rhigozum trichotomum	14,4	33,5	1,49	0,25	2,23	14,8	34,1	0,97	0,22	0,51
	15,3	31,5	1,42	0,19	2,66	12,0	31,5	1,20	0,27	0,35
	8,0	37,6	1,73	0,25	1,41	13,3	42,8	0,58	0,20	0,17
Searsia burchelli	11,0	34,7	2,23	0,36	1,48	13,0	37,3	1,12	0,33	0,45
	12,5	34,2	1,85	0,69	1,72	11,8	37,8	1,39	0,35	0,42
	9,7	35,9	2,52	0,41	1,01	10,7	35,0	1,57	0,31	0,10
Searsia cilliata	17,4	44,3	1,84	0,65	2,15	15,6	46,6	1,51	0,53	0,19
	18,8	40,7	2,23	0,66	2,25	15,6	46,6	1,51	0,53	0,19
	14,1	44,8	1,87	0,62	1,49	14,2	39,7	1,58	0,58	0,11
Senegalia mellifera	23,8	39,7	4,01	0,62	1,70	24,4	41,2	1,94	0,39	0,25
	18,3	38,7	6,38	0,64	0,76	16,4	34,9	3,15	0,37	0,18
	23,3	40,3	5,83	0,56	2,18	26,0	37,5	1,43	0,57	0,30
Tarchonanthus camphoratus	13,5	43,2	1,10	0,45	2,62	13,2	47,9	0,66	0,31	0,40
	12,4	43,6	1,64	0,34	2,87	10,7	47,9	0,89	0,40	0,48
	9,4	45,7	1,20	0,26	2,28	9,1	47,7	0,72	0,28	0,39
Vachellia erioloba	14,7	48,7	2,95	0,45	1,52	17,0	52,5	1,25	0,20	0,12
	14,0	46,9	3,19	0,43	1,46	15,2	50,7	1,39	0,25	0,12
	14,0	44,8	2,21	0,47	1,63	17,6	49,2	0,93	0,17	0,14
Vachellia haematoxylon	12,7	60,9	1,36	0,30	1,96	13,9	61,9	0,72	0,16	0,34
	13,1	58,3	1,55	0,31	1,66	14,2	60,0	1,27	0,32	0,37
	12,3	59,8	2,51	0,47	1,24	14,3	50,0	0,76	0,20	0,10
Vachellia herbaclada	18,6	50,4	3,83	0,54	1,93	20,9	52,9	1,35	0,28	0,42
	13,6	45,2	5,08	0,76	1,35	13,6	45,2	2,43	0,37	0,37
	23,4	46,6	1,97	0,40	4,30	24,3	42,8	0,89	0,32	0,25
Vachellia karroo	13,5	38,7	4,32	0,62	1,14	16,1	38,4	1,03	0,38	0,36
	11,9	37,8	5,06	0,67	1,14	13,8	35,6	2,07	0,40	0,37
	21,9	38,5	1,29	0,37	3,26	20,8	33,2	0,50	0,23	0,24
Ziziphus mucronata	18,6	38,1	2,25	0,54	1,83	18,1	38,4	1,56	0,25	0,40
	14,8	29,8	3,02	0,49	1,26	12,6	31,1	1,31	0,30	0,35
	14,1	33,3	3,43	0,57	1,54	19,4	32,0	1,02	0,31	0,28
V. haematoxyl x V. erioloba	13,6	52,6	2,28	0,39	1,73	15,2	55,7	1,27	0,26	0,13
	13,8	50,3	2,98	0,51	1,24	14,7	49,0	1,46	0,28	0,11
	13,5	47,3	4,38	0,52	1,12	16,6	41,9	1,43	0,23	0,16

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Appendix B. The concentration of all elements in grass species studies, starting with the wet season concentrations (top value), early wet season (mid value) and late dry season concentration (bottom value).

Species	During drought					After drought				
	CP	NDF	C	Mg	P	CP	NDF	C	Mg	P
Anthephora argeta	7,3	70,2	0,38	0,30	0,08	3,7	81,0	0,28	0,21	0,11
	3,5	76,7	0,42	0,38	0,04	2,9	78,3	0,23	0,23	0,16
	5,5	65,9	0,39	0,26	0,07	2,4	76,8	0,16	0,20	0,15
Aristida congesta	6,1	78,2	0,56	0,15	0,03	4,6	84,1	0,18	0,08	0,17
	3,5	83,6	0,36	0,14	0,05	3,4	81,2	0,18	0,09	0,35
	1,6	73,8	0,14	0,03	0,01	1,9	78,7	0,19	0,06	0,30
Aristida diffusa	9,1	78,9	0,38	0,15	0,07	4,8	82,9	0,21	0,15	0,22
	4,1	80,0	0,25	0,12	0,04	3,2	79,5	0,23	0,13	0,25
	2,9	74,7	0,27	0,07	0,03	3,3	79,0	0,15	0,09	0,34
Aristida meriodinalis	6,5	82,5	0,34	0,12	0,09	2,8	85,2	0,18	0,08	0,14
	3,3	81,3	0,39	0,07	0,05	2,8	83,6	0,13	0,06	0,24
	3,3	75,9	0,23	0,07	0,04	3,2	81,3	0,17	0,07	0,19
Aristida stipitata	5,7	82,6	0,26	0,08	0,06	4,5	83,0	0,15	0,08	0,21
	4,2	81,8	0,31	0,11	0,06	3,3	81,9	0,16	0,09	0,37
	3,8	77,0	0,29	0,09	0,05	3,1	78,4	0,18	0,06	0,32
Brachiaria dura	6,1	82,4	0,08	0,10	0,11	3,4	84,6	0,14	0,10	0,16
	4,4	78,8	0,31	0,13	0,04	3,2	84,4	0,09	0,08	0,27
	3,4	80,0	0,15	0,10	0,04	4,5	83,1	0,14	0,08	0,31
Brachiaria nigropedata	12,0	69,1	0,82	0,67	0,09	7,2	72,5	0,34	0,22	0,18
	8,4	71,9	0,63	0,30	0,06	6,5	74,8	0,39	0,22	0,34
	7,7	66,4	0,66	0,21	0,06	3,0	75,1	0,28	0,12	0,18
Cenchrus ciliaris	14,9	64,5	0,41	0,36	0,18	8,3	74,3	0,31	0,34	0,24
	7,1	72,4	0,35	0,36	0,09	5,4	73,8	0,25	0,23	0,26
	7,0	70,2	0,47	0,22	0,08	6,1	74,3	0,19	0,25	0,36
Centropodia glauca	8,9	68,8	1,07	0,24	0,13	4,9	76,9	0,52	0,07	0,26
	4,8	74,2	1,54	0,26	0,03	4,3	77,9	0,55	0,18	0,27
	3,9	70,0	1,37	0,23	0,04	4,3	74,3	0,50	0,15	0,33
Cymbopogon pospischilii	7,3	66,4	0,38	0,25	0,06	3,6	73,6	0,25	0,08	0,11
	4,5	69,4	0,31	0,10	0,04	2,0	79,2	0,15	0,07	0,27
	3,7	69,7	0,52	0,21	0,03	3,3	69,1	0,30	0,09	0,20
Digitaria eriantha	11,9	66,2	0,65	0,70	0,13	5,6	73,9	0,37	0,26	0,20
	7,1	71,1	0,72	0,62	0,05	3,9	77,6	0,35	0,24	0,14
	2,8	70,3	0,66	0,15	0,03	2,8	75,6	0,32	0,25	0,18
Elionurus muticus	8,7	64,3	0,35	0,24	0,08	5,1	71,3	0,29	0,16	0,13
	5,7	72,7	0,59	0,23	0,06	3,9	71,1	0,30	0,12	0,34
	3,7	63,6	0,53	0,17	0,03	3,1	69,3	0,29	0,15	0,17
Eragrostis chloromelas	12,0	77,8	0,44	0,22	0,11	6,8	81,3	0,24	0,12	0,15
	5,4	78,8	0,47	0,13	0,04	4,1	82,8	0,29	0,11	0,14
	5,5	74,5	0,40	0,12	0,05	3,3	79,1	0,22	0,12	0,19
Eragrostis pallens	8,3	80,1	0,49	0,15	0,08	3,2	84,8	0,19	0,07	0,16
	4,0	82,5	0,31	0,10	0,04	3,2	80,3	0,21	0,09	0,29
	4,0	78,9	0,49	0,13	0,04	2,8	78,2	0,26	0,07	0,22
Eragrostis trichophora	8,5	75,6	0,38	0,15	0,09	4,7	82,6	0,21	0,03	0,15
	6,4	75,7	0,62	0,20	0,04	2,6	83,0	0,23	0,09	0,24
	3,5	76,4	0,30	0,10	0,03	2,2	82,4	0,31	0,07	0,19
Mellinis repens	6,4	76,1	0,69	0,68	0,06	5,1	76,4	0,33	0,11	0,15
	4,1	77,9	0,46	0,50	0,04	3,8	78,4	0,30	0,34	0,18
	3,6	72,2	0,42	0,28	0,03	2,8	77,7	0,31	0,21	0,15
Panicum kalaharense	14,0	68,1	0,39	0,19	0,12	7,6	75,5	0,23	0,14	0,16
	5,6	74,5	0,35	0,11	0,05	3,7	77,8	0,35	0,12	0,33
	6,4	71,0	0,50	0,13	0,05	3,2	76,6	0,20	0,07	0,22
Schmidtia kalihariensis	9,6	70,7	1,43	0,21	0,24	6,0	76,9	0,52	0,15	0,17
	7,4	65,1	0,74	0,15	0,10	3,5	77,0	0,39	0,09	0,06
	4,3	65,0	0,79	0,13	0,04	2,0	79,6	0,27	0,06	0,24
Stipagrostis amabilis	5,5	81,4	0,51	0,25	0,08	4,1	82,1	0,27	0,09	0,17
	4,7	80,7	0,49	0,09	0,06	4,6	84,6	0,08	0,07	0,10
	4,2	82,4	0,35	0,08	0,09	3,8	82,0	0,10	0,06	0,10
Stipagrostis obtusa	6,3	73,7	0,58	0,13	0,08	5,7	79,4	0,46	0,14	0,17
	4,5	76,5	0,94	0,10	0,04	5,5	78,8	0,38	0,09	0,38
	4,5	71,0	0,54	0,09	0,05	3,5	77,3	0,33	0,08	0,24

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Stipagrostis uniplumis	6,9	80,2	0,55	0,20	0,07	4,1	82,0	0,26	0,05	0,11
	4,2	82,3	0,49	0,10	0,04	3,1	81,3	0,25	0,08	0,26
	3,6	71,9	0,32	0,04	0,04	2,8	77,0	0,28	0,04	0,31

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