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Seasonal variation in chemical composition and in-vitro gas production of woody plant species of semi-arid condition of Namibia

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Abstract Woody plants are essential in ruminant nutrition in semi-arid regions particularly during the long dry season, however, their nutritional value varies considerably among species, seasons and geographical zones. A study was conducted to evaluate the seasonal variation in chemical composition and in-vitro gas production of woody plant leaves and their relationship. Leaves from sixteen (16) major plant species utilized by livestock were collected from six constituencies of Namibia in the wet season (January: summer), early-dry (May: winter) and late-dry (September: spring) season. There were significant influences of seasonal variations on dry matter (DM), ash, neutral detergent fibre (NDF) and soluble tannin (ST) concentrations of the plant species ($p < 0.05$). However, crude protein (CP) and acid detergent fibre (ADF) were not affected by season ($p > 0.05$). *Rhigozum trichotomum* (900 ± 13.9 g/kg), *Vachellia hereroensis* (902 ± 13.8 g/kg) and *Baphia massaiensis* (910 ± 13.2 g/kg) had lower DM content during the late-dry season as compared to wet and early-dry season. The NDF content was highest in *Grewia bicolor* (610 ± 48.1 g/kg DM) in the wet season and lowest in *Vachellia mellifera* (232.0 ± 41.5 g/kg DM) in the early-dry season. Seasonal variation influenced the rate of degradation but not the potential gas production, however, the species were not significantly influenced by seasonal variation for the parameters measured. Species with higher gas potential showed lower rates of degradation (r = − 0.71, $p < 0.01$). Though the chemical composition of the species was poorly correlated ($p > 0.1$) to the in-vitro gas production parameters, a positive correlation existed between ST and degradation rate (r = 0.52; $p < 0.01$). Seasonal variation influences the quality of

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woody plants and therefore, their leaves should be harvested during their optimal nutritious stage to improve livestock productivity.

Keywords Nutritive value · Degradability · Season · Browse · Supplement

Introduction

Woody plants are important feed resources in Southern Africa particularly during the dry season, when grass biomass and quality are low (Mphinyane et al. 2015). Most woody plants remain green in the dry season because their root system enables them to extract water and nutrients from the soil (Gebeyew et al. 2015). Leaves and pods can be harvested when they are in abundance and with optimal nutrient content to be utilised during the dry season, thus maximizing their utilization and improving livestock productivity (Mlambo and Mapiye 2015; Nsubuga et al. 2020). Leguminous woody plant species are also able to fix atmospheric nitrogen, increasing their protein content and soil fertility. Dietary strategies using woody plants have been reported to reduce enteric methane emission (Tirfessa and Tolera 2020; Bouazza et al. 2020).

Southern Africa is characterised by high temperatures and rainfall is highly variable and unevenly distributed, resulting in frequent and recurring drought (Nicholson et al. 2018). Livestock depends on the range vegetation (grasses and woody plants) with crude protein (CP) content ranging from 80–280 g/kg of dry matter (DM) at the beginning of rainy seasons, which drops to 20–40 g/kg in the dry season (Sibanda and Ndlovu 1992; Wesuls et al. 2009), resulting in a prolonged period of undernutrition. Several browse species (leaves and pods) have been evaluated as alternative protein supplements (Tefera et al. 2008; Sebata et al. 2011; Marius et al. 2018; Simbaya et al. 2020) due to feed shortage during the dry season. Moreover, commercial feed supplements are not affordable or may not be accessible by resource-poor farmers.

Reliable techniques have been widely used to determine digestibility and fermentation of the feed using in-vitro dry matter digestibility (Tilley and Terry 1963) and in-vitro gas production procedure (IVGP) (Menke and Steingass 1988) which was later modified by Theodorou et al. (1994). The IVGP technique has been known to be effective in determining nutritive value of woody species which contain phenolic-related antinutritive factors, neutral detergent fibre (NDF) and lignin (Sebata et al. 2011; Khazaal and Ørskov 1994). The amount of gas produced during in-vitro fermentation reflects the extent at which the feed is digested (Getachew et al. 2004), hence the availability of nutrients to the animal. Although browses provide feed for the livestock, they contain anti-nutritional factors which have varied animal response when ingested (Makkar 2003). Seasonal variation influences the nutritional values of browses (Larbi et al.1998; Lukhele and van Ryssen 2003; Mphinyane et al. 2015), however, there have been limited research studies on the effects of season on the nutritional value of woody plants in Namibia. Therefore, this study investigated the seasonal variation on the chemical composition and in-vitro gas production of 16 indigenous woody plant leaves utilised by livestock in Namibia. The study also evaluated the relationships among chemical composition and gas production characteristics.

Materials and methods

Study area

The study was carried out in Gibeon, Guinas, Kongola, Tsandi, Dâures, and Omatako constituencies of Namibia. The study areas are located at different altitudes above sea level since they are spread throughout the country (Fig. 1). The annual rainfall ranges from 100 mm in the south, 400 mm west part to 900 mm north-eastern part of the country. The average temperature ranges from < 3 °C in winter to > 36 °C in summer. The Namibian soils are categorised into two zones; soils derived from rocky areas in the south, central and the western regions; the Kalahari sands dominate the eastern and northern regions (Mendelsohn 2006). The predominant soils in these rocky areas are known as leptosols and regosols and the sands are called arenosols.

Chemical composition of plant samples was conducted at the Directorate of Agricultural Research and Development Laboratory under the Ministry of Agriculture, Water and Lannd Reform (MAWLR), Windhoek, Namibia. Whereass, in-vitro gas production was conducted at Department of Animal Science Forage Laboratory, University for Development Studies, Nyankpala Campus in Tamale, Ghana.

Collection and preparation of leave samples

The major trees and shrubs utilized by livestock in the study areas were identified in a survey by Marius et al. (2017). Sixteen (16) plant species namely; *Vachellia mellifera*, *Vachellia karroo*, *Vachellia hereroensis*, *Dichrostachys cinerea*, *Grewia bicolor*, *Combretum apiculatum*, *Combretum collinum*, *Philenoptera nelsii*, *Terminalia prunioides*, *Terminalia sericea*, *Colophospermum mopane*, *Baphiam massaiensis*, *Bauhinia petersiana*, *Catophractes alexandri*, *Rhigozum trichotomum* and *Ziziphus mucronata* were identified and therefore used in this study. Leaves from woody plants were collected in three periods, following the seasonal vegetation changes; January (wet season i.e. summer), May (early-dry season i.e. winter) and September (late-dry season i.e. spring) in 2014. In each season per study location, samples were collected randomly from 10 different plants for each species by hand and mixed in a khaki paper bag. Subsamples were taken and dried under a well-ventilated room. Samples were transported to the laboratory and oven dried at 60–70 °C for 12 h. Dried samples were ground to pass through 1 mm sieve and stored in air-tight plastic containers for subsequent analyses.

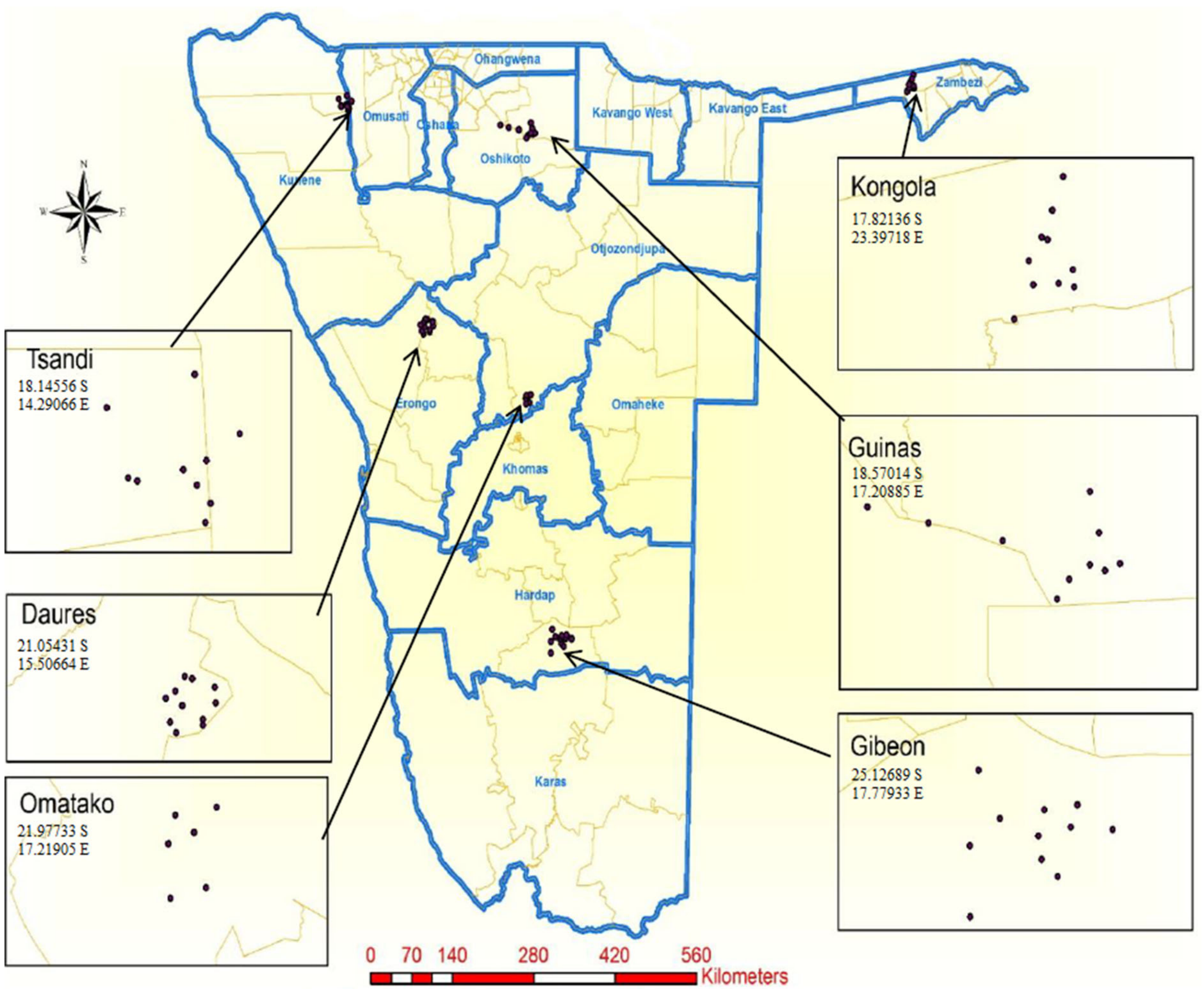

Fig. 1 Map of Namibia showing constituencies coordinates in each region

Chemical composition analysis

Dry matter content of the browse was determined by placing the sample in the oven at 105 °C for 24 h (AOAC 2007). Total ash was obtained by igniting the samples in a muffle furnace at 550 °C for 6 h. Crude protein (CP) was determined by method no. 978.04 of AOAC (2007) and CP was calculated by multiplying nitrogen content by a factor 6.25. The NDF and ADF was determined as described by Robertson and van Soest (1981). Water soluble tannins (ST) were extracted from fat free samples in 70% aqueous acetone extraction followed by colorimetric determination using Folin and Ciocalteau phenol reagent method (Gutfinger 1981).

In-vitro digestibility

The in-vitro gas production was determined following the procedure of Theodorou et al. (1994). Rumen digesta was collected from two male slaughtered West African Shorthorn cattle after a starvation period of 12 h. At carcass opening, ruminal contents were immediately collected into a flask and transported to the laboratory filtered through four layers of cheesecloth, homogenized and kept at 39 °C in the water bath under continuous flushing with CO_2 before use. A litre of rumen fluid was diluted with 4 L of buffer solution containing Menke and Steingass (1988) reagent (macro, micro minerals, and buffer and reduction solution). Culture bottles were filled with 0.2 g of dried sample, 30 ml of solution and placed into a 39 °C water bath. Gas production data were recorded after 3, 6, 9, 12, 24, 36 and 48 h of incubation, gently shaking each bottle every 3 h. There were 5 batches of 48 h of fermentation with 77 units in each, including a blank culture bottle for correction purposes. A digital manometer device (Product: HT-1895, China) was used to measure the gas pressure in pounds per square inch (psi). Gas volume was obtained by applying Boyle's law (López et al. 2007) using the expression:

$$y(ml) = Vh/P_a \times P_t$$

where y = the volume of gas production recorded in the culture bottle, V_h = the headspace volume, P_a = the atmospheric pressure, and P_t = pressure measured at time *t*.

Statistical analysis

Since the study locations are spread throughout the country, some plant species were confined to certain study locations (Table 1). Therefore, location effect was ignored, as it could not be effectively separated from species effect.

Concentrations of DM, ash, CP, NDF, ADF and ST were analysed with beta generalized linear models with logit link, using the following statistical model:

$$Y \sim \beta\{\exp(\eta)/[1+\exp(\eta)], \varphi\}$$

$$\eta = \mu + S_i + P_j + (SP)_{ij}$$

where Y is the observation (proportion of each nutrient from 0 to 1, φ is the scale parameter for Beta distribution, η is the linear predictor, μ is the overall mean, S_i is the effect of the i-th species, P_j is the effect of the j-th season, $(SP)_{ij}$ is the season * species interaction.

Each sample was considered the statistical unit. After both nutrient concentration and in-vitro gas production models were fitted, means for different species on the same season were compared pairwise, declaring significant differences when $p < 0.05$ and trends when $p < 0.10$. Seasonal effects within species were evaluated using orthogonal polynomial contrasts, as evaluations were approximately equally spaced (4 months between observations) and it could be interesting to determine the behaviour of variables evaluated throughout the year.

In-vitro gas production was analysed using non-linear mixed effects models. Gas volume readings were fitted to the exponential equation $y = b\{1\text{-}\exp[-\exp(c)t]\}$, where *y* denotes the cumulative gas production at time *t*, *b* is the potential gas production, and *c*, the log transformed rate of gas production. Random effects for sample, subsample nested in the sample, and observation nested in subsample were included to consider correlation due to multilevel structure of the data (5 replicates by sample, 6 measurements by replicate). To account for temporal autocorrelation between measurements, several plausible covariance structures were tested, checking their appropriateness by inspection of the residual autocorrelation function (ACF) and comparing Akaike Information Criteria (AIC) for each candidate model. Finally, an unstructured covariance matrix was selected. Fixed effects of

Table 1 Species collection at each sampling location

Species	Sampling Location (Constituencies)					
	Gibeon	Guinas	Kongola	Tsandi	Dâures	Omatako
V. hereroensis					x	
V. karoo					x	
V. mellifera	x					
B. massiensis			x			
B. petersiana		x	x			
C. alexandri	x			x	x	
C. apiculatum				x		x
C. collinum			x			
C. mopane				x		
D. cinerea		x				
G. bicolor		x				
P. nelsii		x	x	x		
R. trichotomum	x					
T. prunioides				x		
T. sericea		x	x	x		
Z. mucronata						x

x = specie collected at specific location

species, month and their interaction were calculated for parameters *b* and *c*.

As an additional analysis, Pearson correlation coefficients were calculated to assess the linear relationship between gas production curve parameters and chemical composition. All statistical analyses were performed on R, version 3.6.3, using packages *betareg* (Cribari-Neto and Zeileis 2010) for beta regression and *nlme* (Pinheiro et al. 2018) for non-linear mixed models. *p*-values for pairwise comparisons, orthogonal contrasts and correlation coefficients were corrected by Benjamini and Hochberg (1995) procedure (false positive rate).

Results

Chemical composition of woody plants

DM, ash and CP contents of plant leaves harvested in wet, early-dry and late-dry season are presented in Table 2. DM varied significantly between seasons but not among species. There was a significant linear trend ($p < 0.05$) in the DM of most plant species with lower content during the late-dry season as compared to wet and early-dry season. Exceptions for this behaviour were *V. mellifera*, *B. petersiana*, *C. mopane*, *C. collinum*, *G. bicolor*, and *Z. mucronata* as their values did not show significant variation across seasons. Additionally, *V. hereroensis*, *B. massaiensis*, and *R. trichotomum* had significant quadratic trends ($p < 0.05$).

Ash contents were significantly affected by season and species ($p < 0.05$) and tended to be affected by their interaction ($p < 0.10$). During the wet season, *Z. mucronata* showed 3.7 times the ash content of *B. massaiensis*. These species also showed the more extreme values during the early-dry season, when *Z. mucronata* ash content was 3.25 times the one of *B. massaiensis.* Finally, no significant differences were found during the late-dry season. Additionally, a quadratic trend was detected for *P. nelsii*, having higher values in the early-dry season.

CP was not significantly affected by season and species but a significant interaction term was observed ($p < 0.05$). This is reflected in the absence of significant trends over seasons, as well as lack of significant differences for species in the entire dry season (both early and late). On contrary, CP mean values observed in the wet season can be classified in three groups: *T. sericea*, *P. nelsii*, *D. cinerea*, *C. apiculatum*, and *B. petersiana* with high CP (130–140 g/kg); *C. mopane* and *G. bicolor* with low CP contents (around 24–26 g/kg) and the rest having intermediate CP values.

Table 2 DM, ash and CP contents of leaves of woody plant harvested in wet, early-dry and late-dry season

Variable (g/kg)	Species	Seasons[1]			Season Contrasts[2]	
		Wet	Early-dry	Late-dry	Linear	Quadratic
DM	*V. hereroensis*	965 ± 8.4^{a}	962 ± 8.8^{a}	902 ± 13.8^{a}	0.0010	0.0424
	V. karroo	970 ± 7.8^{a}	955 ± 9.5^{a}	934 ± 11.5^{a}	0.0299	0.8061
	V. mellifera	966 ± 8.3^{a}	955 ± 9.5^{a}	939 ± 11.1^{a}	0.0897	0.8061
	B. massaiensis	973 ± 7.4^{a}	969 ± 7.9^{a}	910 ± 13.2^{a}	0.0008	0.0313
	B. petersiana	964 ± 6.0^{a}	964 ± 6.1^{a}	946 ± 7.4^{a}	0.0897	0.3870
	C. alexandri	958 ± 5.3^{a}	951 ± 5.7^{a}	926 ± 7.0^{a}	0.0016	0.2884
	C. mopane	953 ± 9.7^{a}	964 ± 8.5^{a}	931 ± 11.7^{a}	0.2233	0.0897
	C. apiculatum	970 ± 5.5^{a}	954 ± 6.8^{a}	932 ± 8.2^{a}	0.0012	0.7552
	C. collinum	962 ± 8.8^{a}	960 ± 9.0^{a}	949 ± 10.2^{a}	0.4035	0.7552
	D. cinerea	959 ± 9.1^{a}	963 ± 8.7^{a}	916 ± 12.9^{a}	0.0197	0.0738
	G. bicolor	965 ± 8.4^{a}	959 ± 9.1^{a}	935 ± 11.4^{a}	0.0750	0.5062
	P. nelsii	963 ± 5.0^{a}	962 ± 5.1^{a}	936 ± 6.5^{a}	0.0037	0.1008
	R. trichotomum	965 ± 8.4^{a}	963 ± 8.7^{a}	900 ± 13.9^{a}	0.0008	0.0299
	T. prunioides	963 ± 8.6^{a}	951 ± 9.9^{a}	914 ± 13.0^{a}	0.0075	0.4035
	T. sericea	957 ± 6.6^{a}	950 ± 5.8^{a}	930 ± 6.8^{a}	0.0174	0.4871
	Z. mucronata	957 ± 9.3^{a}	953 ± 9.7^{a}	931 ± 11.7^{a}	0.1173	0.5062
Ash	*V. hereroensis*	72 ± 14.7^{ab}	90 ± 16.3^{abcd}	56 ± 13.0^{a}	0.7056	0.6208
	V. karroo	71 ± 14.6^{ab}	69 ± 14.3^{abcd}	55 ± 12.9^{a}	0.7056	0.9501
	V. mellifera	84 ± 15.7^{ab}	114 ± 18.1 ^{cd}	63 ± 13.7^{a}	0.6445	0.2638
	B. massaiensis	27 ± 9.1^{a}	40 ± 11.1^{a}	63 ± 13.7^{a}	0.2239	0.9501
	B. petersiana	54 ± 9.0^{ab}	80 ± 10.9^{abcd}	70 ± 10.2^{a}	0.6445	0.6208
	C. alexandri	62 ± 7.9^{ab}	66 ± 8.1^{abc}	68 ± 8.3^{a}	0.8342	0.9946
	C. mopane	51 ± 12.4^{ab}	48 ± 12.1^{ab}	72 ± 14.6^{a}	0.6445	0.7056
	C. apiculatum	60 ± 9.5^{ab}	59 ± 9.5^{abc}	60 ± 9.5^{a}	0.9946	0.9946
	C. collinum	67 ± 14.1^{ab}	52 ± 12.6^{abc}	56 ± 12.9^{a}	0.8342	0.8342
	D. cinerea	61 ± 13.6^{ab}	56 ± 13.0^{abc}	67 ± 14.2^{a}	0.9501	0.8342
	G. bicolor	81 ± 15.5^{ab}	69 ± 14.4^{abcd}	58 ± 13.2^{a}	0.6445	0.9946
	P. nelsii	65 ± 8.1^{ab}	89 ± 9.4^{bcd}	43 ± 6.6^{a}	0.2239	0.0343
	R. trichotomum	76 ± 15.0^{ab}	85 ± 15.8^{abcd}	54 ± 12.8^{a}	0.6445	0.6445
	T. prunioides	81 ± 15.5^{ab}	69 ± 14.3^{abcd}	61 ± 13.5^{a}	0.6445	0.9946
	T. sericea	51 ± 8.8^{ab}	65 ± 8.0^{abc}	50 ± 7.1^{a}	0.9946	0.6208
	Z. mucronata	100 ± 17.0^{b}	130 ± 19.1^{d}	42 ± 11.3^{a}	0.0736	0.0736
CP	*V. hereroensis*	48 ± 24.6^{ab}	50 ± 25.2^{a}	117 ± 38.7^{a}	0.6089	0.6370
	V. karroo	120 ± 39.1^{ab}	98 ± 35.6^{a}	147 ± 43.0^{a}	0.8446	0.6705
	V. mellifera	133 ± 41.1^{ab}	145 ± 42.7^{a}	85 ± 33.1^{a}	0.6370	0.6705
	B. massaiensis	80 ± 32.1^{ab}	154 ± 43.8^{a}	61 ± 28.0^{a}	0.8524	0.5434
	B. petersiana	140 ± 29.7^{b}	75 ± 22.1^{a}	157 ± 31.2^{a}	0.8574	0.2484
	C. alexandri	71 ± 17.5^{ab}	153 ± 25.2^{a}	77 ± 18.2^{a}	0.8959	0.1574
	C. mopane	26 ± 17.1^{a}	82 ± 32.6^{a}	81 ± 32.3^{a}	0.6089	0.6705
	C. apiculatum	130 ± 28.7^{b}	102 ± 25.7^{a}	121 ± 27.8^{a}	0.8959	0.6705
	C. collinum	31 ± 19.2^{a}	140 ± 42.0^{a}	79 ± 32.0^{a}	0.6366	0.5273
	D. cinerea	173 ± 46.0^{b}	91 ± 34.2^{a}	98 ± 35.6^{a}	0.6366	0.6370
	G. bicolor	24 ± 16.0^{a}	123 ± 39.6^{a}	119 ± 39.0^{a}	0.2484	0.6370

Table 2 continued

Variable (g/kg)	Species	Seasons[1]			Season Contrasts[2]	
		Wet	Early-dry	Late-dry	Linear	Quadratic
	P. nelsii	136 ± 23.9[b]	90 ± 19.7[a]	96 ± 20.3[a]	0.6366	0.6370
	R. trichotomum	97 ± 35.4[ab]	56 ± 26.8[a]	103 ± 36.4[a]	0.9391	0.6370
	T. prunioides	106 ± 37.0[ab]	74 ± 30.9[a]	117 ± 38.7[a]	0.8959	0.6370
	T. sericea	130 ± 28.8[b]	93 ± 20.0[a]	95 ± 20.2[a]	0.6370	0.6705
	Z. mucronata	99 ± 35.8[ab]	108 ± 37.3[a]	97 ± 35.4[a]	0.9717	0.8959

[1]Different superscripts indicate $p < 0.05$ for species pairwise contrasts in the same season, after Benjamini & Hochberg multiplicity adjustment

[2]p-values for polynomic trends on the same species across seasons, after Benjamini & Hochberg adjustment

Cell wall components and ST contents of plant leaves harvested in wet, early-dry and late-dry season are presented in Table 3. Although ADF was not affected by season, species and their interaction, NDF content was affected by season, species and their interaction ($p < 0.001$ for all). A significant linear trend ($p < 0.05$) in NDF was observed in *G. bicolor* and *P. nelsii*, with the highest NDF in the wet season. On contrary, *V. hereroensis* had the highest NDF in early-dry (477 ± 49.3 g/kg DM) and late-dry (440 ± 49.0 g/kg DM) season than in the wet season (247 ± 42.4 g/kg DM). Furthermore, although significant differences were observed during wet and early-dry seasons, during late-dry all analysed materials showed similar NDF contents.

The ST contents were affected by season ($p < 0.05$), species ($p < 0.0001$) but not their interaction. During the wet and early-dry season, there were no significant differences between species, however, during late-dry season, ST content in *C. apiculatum* was 1.5 to 4 times higher than other species in the same season. No significant trends for season were encountered.

In-vitro gas production of woody plants

In-vitro gas production of woody plant leaves harvested in wet, early-dry and late-dry season are shown in Table 4. Potential gas production (*b*) was affected by species ($p < 0.0001$) but not by season or species * season interaction. In the early-dry season, *V. mellifera* produced the highest gas while *C. collinum* and *C. apiculatum* had the lowest. *V. mellifera* and *Z. mucronata* had the highest gas production in the late-dry season, which was 2.5 times more than the gas produced by *D. cinerea*, being the lowest gas produced. Based on the potential gas production data, three groups was established: a group of species with low values (*C. mopane*, *D. cinerea*, *C. apiculatum*, *C. collinum*) with *b* values mostly from 4 to 7; a group with high gas production potential, with values above 10 (*V. mellifera*, *C. alexandri*, and *Z. mucronata*); and a third group with intermediate values containing all other species.

In a similar way, the rate of degradation (*c*) also differed significantly between species ($p < 0.0001$), season ($p < 0.05$) and a significant species*season interaction ($p < 0.05$) was registered. It changed from − 2.7 in *V. mellifera* to − 1.6 in *C. apiculatum* during the wet season, with most species showing values below − 2.0. The lowest value in early-dry season was − 2.7 and it was reached by *Z. mucronata*, while the highest was observed in *C. collinum* (− 1.2). In the late-dry season, the highest value was − 1.5 in *C. collinum*, well over the − 2.7 of *Z. mucronata.* No significant ($p > 0.05$) linear nor quadratic contrasts for species were found after multiplicity correction.

Correlations between chemical composition and in-vitro gas production

Correlation coefficients between chemical composition and in-vitro gas production parameters are presented in Table 5. Gas production parameters were significantly ($p < 0.05$), but negatively correlated, implying that samples with higher values for potential

Table 3 The NDF, ADF and soluble tannins of woody plant leaves harvested in wet, early-dry and late-dry season

Variable	Species	Seasons[1]			Season Contrasts[2]	
		Wet	Early-dry	Late-dry	Linear	Quadratic
NDF (g/kg)	*V. hereroensis*	247 ± 42.4^{a}	477 ± 49.3^{cd}	440 ± 49.0^{a}	0.0304	0.0976
	V. karroo	407 ± 48.5^{bcde}	361 ± 47.4^{abcd}	374 ± 47.8^{a}	0.6947	0.6947
	V. mellifera	298 ± 45.1^{abc}	232 ± 41.5^{a}	343 ± 46.8^{a}	0.6077	0.3033
	B. massaiensis	491 ± 49.4^{def}	421 ± 48.8^{bcd}	406 ± 48.5^{a}	0.3554	0.6947
	B. petersiana	463 ± 34.8^{de}	370 ± 33.7^{abcd}	395 ± 34.1^{a}	0.3404	0.3404
	C. alexandri	420 ± 28.1^{cde}	382 ± 27.7^{bcd}	395 ± 27.9^{a}	0.6300	0.6049
	C. mopane	353 ± 47.1^{abcde}	369 ± 47.6^{abcd}	429 ± 48.9^{a}	0.3942	0.7316
	C. apiculatum	357 ± 33.4^{abcd}	252 ± 30.2^{a}	427 ± 34.5^{a}	0.3404	0.0088
	C. collinum	306 ± 45.4^{abc}	289 ± 44.7^{ab}	394 ± 48.2^{a}	0.3404	0.3942
	D. cinerea	498 ± 49.4^{ef}	412 ± 48.6^{bcd}	519 ± 49.3^{a}	0.7690	0.3093
	G. bicolor	610 ± 48.1^{f}	429 ± 48.9^{bcd}	405 ± 48.5^{a}	0.0304	0.3404
	P. nelsii	574 ± 28.2^{f}	475 ± 28.5^{d}	464 ± 28.4^{a}	0.0463	0.3404
	R. trichotomum	303 ± 45.3^{abc}	310 ± 45.6^{abc}	438 ± 49.0^{a}	0.1552	0.3985
	T. prunioides	336 ± 46.6^{abcd}	273 ± 43.9^{ab}	502 ± 49.4^{a}	0.0750	0.0542
	T. sericea	488 ± 34.9^{ef}	374 ± 27.6^{bcd}	423 ± 28.2^{a}	0.3404	0.0976
	Z. mucronata	275 ± 44.0^{ab}	358 ± 47.3^{abcd}	360 ± 47.4^{a}	0.3404	0.6077
ADF (g/kg)	*V. hereroensis*	172 ± 82.5^{a}	165 ± 80.9^{a}	279 ± 100.9^{a}	0.9615	0.9615
	V. karroo	244 ± 96.0^{a}	221 ± 92.4^{a}	232 ± 94.2^{a}	0.9615	0.9615
	V. mellifera	219 ± 92.0^{a}	239 ± 95.3^{a}	311 ± 104.6^{a}	0.9615	0.9615
	B. massaiensis	344 ± 107.8^{a}	125 ± 70.2^{a}	319 ± 105.4^{a}	0.9615	0.7211
	B. petersiana	323 ± 74.9^{a}	316 ± 74.4^{a}	318 ± 74.5^{a}	0.9615	0.9615
	C. alexandri	319 ± 60.9^{a}	348 ± 62.4^{a}	309 ± 60.3^{a}	0.9615	0.9615
	C. mopane	270 ± 99.8^{a}	272 ± 100.1^{a}	338 ± 107.2^{a}	0.9615	0.9615
	C. apiculatum	276 ± 71.1^{a}	200 ± 62.6^{a}	298 ± 73.0^{a}	0.9615	0.9615
	C. collinum	233 ± 94.4^{a}	258 ± 98.1^{a}	347 ± 108.0^{a}	0.9615	0.9615
	D. cinerea	267 ± 99.4^{a}	338 ± 107.3^{a}	358 ± 108.9^{a}	0.9615	0.9615
	G. bicolor	322 ± 105.8^{a}	317 ± 105.3^{a}	252 ± 97.3^{a}	0.9615	0.9615
	P. nelsii	425 ± 65.1^{a}	374 ± 63.5^{a}	294 ± 59.4^{a}	0.9615	0.9615
	R. trichotomum	230 ± 93.9^{a}	184 ± 85.2^{a}	243 ± 95.9^{a}	0.9615	0.9615
	T. prunioides	374 ± 110.0^{a}	302 ± 103.7^{a}	256 ± 97.9^{a}	0.9615	0.9615
	T. sericea	299 ± 73.1^{a}	521 ± 65.8^{a}	342 ± 62.1^{a}	0.9615	0.4307
	Z. mucronata	175 ± 83.1^{a}	183 ± 85.0^{a}	266 ± 99.3^{a}	0.9615	0.9615
ST (g/100 g)	*V. hereroensis*	2.8 ± 1.98^{a}	5.8 ± 3.11^{a}	4.2 ± 2.57^{a}	0.8824	0.8795
	V. karroo	2.0 ± 1.57^{a}	3.5 ± 2.29^{a}	4.0 ± 2.49^{a}	0.8795	0.9396
	V. mellifera	2.9 ± 2.03^{a}	4.6 ± 2.71^{a}	4.2 ± 2.57^{a}	0.8824	0.8824
	B. massaiensis	5.5 ± 3.01^{a}	4.3 ± 2.60^{a}	8.0 ± 3.73^{ab}	0.8795	0.8795
	B. petersiana	4.4 ± 1.85^{a}	5.9 ± 2.21^{a}	7.3 ± 2.50^{ab}	0.8795	0.9849
	C. alexandri	3.3 ± 1.26^{a}	5.6 ± 1.75^{a}	5.3 ± 1.70^{a}	0.8795	0.8795
	C. mopane	6.4 ± 3.29^{a}	5.8 ± 3.11^{a}	11.6 ± 4.54^{ab}	0.8795	0.8795
	C. apiculatum	8.4 ± 2.70^{a}	10.5 ± 3.05^{a}	21.4 ± 4.44^{b}	0.3925	0.8795
	C. collinum	7.6 ± 3.62^{a}	9.4 ± 4.05^{a}	4.9 ± 2.82^{a}	0.8795	0.8795
	D. cinerea	2.9 ± 2.03^{a}	7.3 ± 3.54^{a}	4.9 ± 2.82^{a}	0.8795	0.8795
	G. bicolor	2.6 ± 1.89^{a}	5.7 ± 3.08^{a}	3.6 ± 2.33^{a}	0.8824	0.8795

Table 3 continued

Variable	Species	Seasons[1]			Season Contrasts[2]	
		Wet	Early-dry	Late-dry	Linear	Quadratic
	P. nelsii	2.2 ± 0.97[a]	4.8 ± 1.59[a]	3.8 ± 1.38[a]	0.8795	0.8795
	R. trichotomum	2.9 ± 2.03[a]	5.5 ± 3.01[a]	7.4 ± 3.57[ab]	0.8795	0.9520
	T. prunioides	12.6 ± 4.77[a]	10.5 ± 4.30[a]	14.9 ± 5.21[ab]	0.8824	0.8795
	T. sericea	10.4 ± 3.04[a]	11.1 ± 2.57[a]	9.9 ± 2.41[ab]	0.9418	0.8827
	Z. mucronata	2.5 ± 1.84[a]	5.1 ± 2.88[a]	4.1 ± 2.53[a]	0.8795	0.8795

[1]Different superscripts indicate $p < 0.05$ for species pairwise contrasts on the same season, after Benjamini & Hochberg multiplicity adjustment

[2]p-values for polynomic trends on the same species across seasons, after Benjamini & Hochberg adjustment

gas production (*b*) showed concomitantly lower rates of gas production (*c*). Overall, chemical composition of the woody plant species was poorly correlated to the in-vitro gas production parameters, except for ash and ST. While *b* was positively correlated with ash (r = 0.343, $p < 0.05$) but negatively correlated with ST contents (r = − 0.315; $p < 0.10$), higher values for the natural logarithm of the gas production rates are expected as ST increases (r = 0.522, $p < 0.001$). Additional significant correlation was found between ADF and NDF.

Discussion

The nutritive values of browse plants vary greatly depending on the species, season and geographical zones. Chemical composition of the analysed woody species was comparable to the values reported by other authors (Larbi et al. 1998; Lukhele and Ryssen 2003; Mlambo et al. 2008 and Sebata et al. 2011). Most species showed lower DM values during the late-dry season as compared to wet and early-dry season. This result could be due to the time of harvesting of leaves with little effects on their leaf development because of prolonged dry season and delayed rainfall. Typically, DM increases as the plant matures and as the dry season advances (Mueller-Harvey 2006).

The NDF concentrations were within the range of those reported by van Soest (1994) and varied among woody species due to differences in cell wall structures. However, a higher NDF content in wet season than in dry season recorded in some woody species in this study contrasts with the expected behaviour, whereby NDF and lignin increase in dry season (Khazaal and Ørskov 1994). As the season advances and plant matures, the protein content decreases, while fibre and tannin levels increase (Mueller-Harvey 2006; Nsubuga et al. 2020). Possible reasons for this study results were delayed and low rainfall and that leaves collected could be remnants of the previous season, as suggested by Marius (2016), that indicated that some woody species, such as *C. mopane*, *V. karoo*, *Z. mucronata*, *B. massaiensis*, and *B. petersiana;* are able to cope through the winter and maintain their leaves into the dry season.

Variation in ST contents between woody species and seasons observed in this study is consistent with Khazaal and Ørskov (1994). Mlambo et al. (2008) reported higher phenolic and tannin content in *D. cinerea* and *Vachellia* spp. leaves and fruits of Southern Africa. The higher concentration of ST in the late-dry season as compared to the wet season observed in most woody species could be attributed to the browsing intensity, the stage of plant growth and seasonal changes (Mueller-Harvey 2006). Ruminants tend to browse more in the dry season when the grazing resources are scarce, and this coincides with increased fibre and tannins values. Plants synthesized tannins as a defence mechanism against herbivores (Mueller-Harvey and McAllan 1992) especially when the plant is frequently disturbed. Makkar (2003) reported other factors such as the quantity of tannins in woody leaves could be susceptible to change during initial harvesting, drying temperature and extraction method and therefore could reduce digestibility.

Table 4 In-vitro gas production parameters estimated for woody plant leaves harvested in wet, early-dry and late-dry season

Species	Season						Season Contrasts[1]			
	Wet		Early-dry		Late-dry		Linear		Quadratic	
	b^2	c^3	b^2	c^3	b^2	c^3	b^2	c^3	b^3	c^3
V. hereroensis	9.4 ± 1.78^{abcd}	− 2.4 ± 0.22^{ab}	12.1 ± 1.79^{abc}	− 2.6 ± 0.21^{ab}	8.0 ± 1.78^{ab}	− 2.4 ± 0.23^{ab}	0.9460	0.9851	0.7879	0.7611
V. karroo	7.2 ± 1.78^{abc}	− 2.5 ± 0.24^{ab}	9.1 ± 1.79^{abc}	− 2.2 ± 0.23^{abc}	7.7 ± 1.79^{ab}	− 1.9 ± 0.23^{ab}	0.9550	0.3710	0.9338	0.9851
V. mellifera	12.3 ± 1.78^{bcd}	− 2.7 ± 0.21^{a}	15.6 ± 1.78^{c}	− 2.8 ± 0.20^{a}	11.4 ± 1.78^{abc}	− 2.5 ± 0.21^{ab}	0.9550	0.7611	0.7879	0.7381
B. massaiensis	5.6 ± 1.79^{ab}	− 2.1 ± 0.24^{abc}	6.2 ± 1.78^{a}	− 2.6 ± 0.25^{ab}	6.7 ± 1.80^{ab}	− 1.6 ± 0.23^{b}	0.9550	0.4565	0.9784	0.2418
B. petersiana	7.3 ± 1.26^{abc}	− 2.4 ± 0.16^{ab}	9.5 ± 1.26^{ab}	− 2.4 ± 0.15^{ab}	6.7 ± 1.27^{a}	− 1.9 ± 0.16^{b}	0.9550	0.2601	0.7879	0.5121
C. alexandri	13.2 ± 1.03^{d}	− 2.5 ± 0.12^{ab}	10.4 ± 1.03^{abc}	− 2.1 ± 0.12^{bc}	11.5 ± 1.06^{bc}	− 2.5 ± 0.12^{a}	0.9338	0.9248	0.7879	0.1927
C. mopane	4.9 ± 1.78^{a}	− 2.3 ± 0.28^{abc}	7.0 ± 1.80^{a}	− 2.0 ± 0.22^{bcd}	6.3 ± 1.80^{ab}	− 1.7 ± 0.23^{b}	0.9460	0.3710	0.9338	0.9851
C. apiculatum	5.8 ± 1.27^{a}	− 1.6 ± 0.17^{c}	6.9 ± 1.27^{a}	− 1.8 ± 0.16^{cd}	7.4 ± 1.27^{ab}	− 2.2 ± 0.15^{ab}	0.9338	0.1927	0.9550	0.8772
C. collinum	4.7 ± 1.80^{a}	− 1.8 ± 0.26^{abc}	6.3 ± 1.78^{a}	− 1.2 ± 0.27^{d}	4.4 ± 1.80^{a}	− 1.5 ± 0.29^{b}	0.9784	0.7381	0.9338	0.5121
D. cinerea	8.6 ± 1.79^{abcd}	− 2.2 ± 0.21^{abc}	6.7 ± 1.80^{a}	− 1.7 ± 0.24^{cd}	6.2 ± 1.79^{ab}	− 1.7 ± 0.24^{b}	0.9338	0.4572	0.9550	0.6546
G. bicolor	7.3 ± 1.78^{abc}	− 2.6 ± 0.24^{ab}	8.0 ± 1.79^{ab}	− 2.3 ± 0.23^{abc}	8.9 ± 1.78^{abc}	− 2.3 ± 0.23^{ab}	0.9338	0.7112	0.9784	0.8772
P. nelsii	9.8 ± 1.03^{abcd}	− 2.4 ± 0.12^{ab}	9.2 ± 1.03^{ab}	− 2.3 ± 0.12^{ab}	6.8 ± 1.04^{a}	− 2.1 ± 0.13^{ab}	0.7879	0.3710	0.9338	0.8621
R. trichotomum	6.2 ± 1.80^{ab}	− 1.8 ± 0.23^{bc}	9.7 ± 1.80^{abc}	− 2.0 ± 0.20^{bcd}	8.9 ± 1.80^{abc}	− 2.0 ± 0.20^{ab}	0.9338	0.8621	0.9338	0.8621
T. prunioides	6.5 ± 1.80^{abc}	− 2.1 ± 0.23^{abc}	7.7 ± 1.80^{ab}	− 2.1 ± 0.21^{bcd}	9.9 ± 1.80^{abc}	− 2.1 ± 0.21^{ab}	0.9319	0.9851	0.9550	0.9851
T. sericea	8.9 ± 1.27^{abcd}	− 2.1 ± 0.15^{abc}	7.1 ± 1.04^{a}	− 1.7 ± 0.13^{cd}	8.4 ± 1.04^{ab}	− 1.9 ± 0.13^{b}	0.9550	0.4565	0.9338	0.3710
Z. mucronata	13.1 ± 1.80^{cd}	− 2.7 ± 0.21^{a}	14.0 ± 1.84^{bc}	− 2.7 ± 0.21^{ab}	15.2 ± 1.78^{c}	− 2.7 ± 0.20^{a}	0.9338	0.9851	0.9784	0.9851

[1]P-values for polynomic trends on the same species across seasons, after Benjamini & Hochberg adjustment

[2]*b*: potential gas production (ml/0.2 g DM)

[3]*c*: natural logarithm of the rate of degradation (/h)

[a,b,c,d]Different superscripts indicate $p < 0.05$ for species pairwise contrasts in the same season and parameter, after Benjamini & Hochberg multiplicity adjustment

Table 5 Correlation coefficients between crude protein, ashes, cell-wall components, soluble tannins and in-vitro gas production curve parameters for woody plant leaves analysed

	In-vitro gas production parameters		DM	Ash	CP	NDF	ADF
	b	c					
c	− 0.71 ($p < 0.01$)						
DM	− 0.06 ($p = 0.77$)	− 0.06 ($p = 0.76$)					
Ash	0.34 ($p = 0.03$)	− 0.29 ($p = 0.08$)	0.24 ($p = 0.20$)				
CP	0.10 ($p = 0.68$)	0.09 ($p = 0.71$)	− 0.01 ($p = 0.96$)	− 0.10 ($p = 0.68$)			
NDF	− 0.02 ($p = 0.92$)	− 0.11 ($p = 0.68$)	− 0.14 ($p = 0.53$)	− 0.23 ($p = 0.23$)	0.07 ($p = 0.75$)		
ADF	− 0.07 ($p = 0.75$)	0.17 ($p = 0.42$)	− 0.09 ($p = 0.71$)	− 0.13 ($p = 0.58$)	0.17 ($p = 0.45$)	0.33 ($p = 0.04$)	
ST	− 0.32 ($p = 0.05$)	0.52 ($p < 0.01$)	− 0.28 ($p = 0.11$)	− 0.11 ($p = 0.68$)	0.04 ($p = 0.81$)	− 0.14 ($p = 0.54$)	0.11 ($p = 0.68$)

CP = Crude protein, NDF = Neutral detergent fibre, ADF = Acid detergent fibre, ST = soluble tannins, b = volume of gas produced, c = rate of gas production; Estimates from the equation: $y = b\,(1 - e^{-\exp(c)t})$, where: b = potential gas production; c = natural logarithm of the rate at which b is degraded

The CP content was not affected by season, inconsistent with the study of Larbi et al. (1998), Melaku et al. (2010) and Abebe et al. (2012). This could be that some woody plants were able to maintain their leaves into the dry season, hence their nutrients, depending on location and grazing pressure (Marius 2016). In this study, *V. hereroensis*, *C. mopane*, *C. collinum* and *G. bicolor* had low to medium CP content and therefore may have little benefit to the animal. According to Mathis et al. (2000), a basal diet containing CP < 70 g/kg could have little benefit to ruminants.

Potential gas production and rate of fermentation were affected by species. Nherera et al. (1999) reported that differences of species and their cell-wall constituents such as NDF, lignin, polyphenolic concentrations and anti-nutritional factors influence the digestibility and degradation characteristics of feeds. A higher gas production potential in *V. mellifera*, *C. alexandri*, and *Z. mucronata* and a lower rate of gas production *C. collinum* may indicate a better nutrient availability for rumen microorganisms, hence digestibility. Getachew et al. (2004) stated that the rate at which different chemical constituents are fermented reflects the microbial growth and accessibility of the feed to microbial enzymes. Moreover, Khazaal and Ørskov (1994) reported that the intake of a feed is mostly explained by the fractional rate of gas production ($k = exp(c)$) which affects the rate of passage of the feed through the gastro-intestinal tract whereas the potential gas production (b) is associated with the degradability of the feed. In this study, the fractional rate of gas production showed little seasonal effect. The non-significant influence of season on the fractional rate of gas production affirms the study by Lukhele and van Ryssen (2003) who reported no significant effect of in-vitro gas production of *Combretum* species leaves with season.

Only ash and ST showed significant correlations ($r = 0.343$, $p < 0.05$ and $r = -0.315$; $p < 0.10$, respectively), with gas production parameters. Plant leaves had low contents of tannins that ranged between 2.0 and 10 g/100 g which would generally be considered unlikely to significantly affect digestion. Though, some species (*C. apiculatum*, *T. prunioides*, and *C. mopane*) had tannin concentration over 11 g/100 g in late-dry season, a period when animals normally browse them, the levels were lower than values over 29 g/100 g reported by Mlambo et al. (2008). Tannins are complex polyphenolics compounds with great structural diversity and influence intake and digestibility of protein in ruminants (Mueller-Harvey 2006). A significant moderate to high correlation was recorded between tannin concentration and the log rate of gas production. This result contrasted the result of Khazaal and Ørskov (1994), who found non-significant correlations between polyphenols and the volume of gas production of the browse species. Larbi et al. (1998) also reported a weak relationship between proanthocyanidins and gas production data of multipurpose trees during the wet and dry season in West Africa. Other possible reasons could be differences in the complex structures of tannins, differences in the fermentation patterns, season, and nutritive value (Abdulrazak et al. 2000).

Conclusions

There was an effect of seasonal variation in DM, ash, NDF and ST of plant species; however, CP and ADF were not affected by species and season. Most plant species could be used as protein supplements, however, *C. mopane* and *G. bicolor* had low CP content and therefore they would not be sufficient protein supplements for ruminants grazing poor quality grass or low-quality diets. Potential gas production was affected by species but not by season or species * season interaction, however, the log rate of degradation differed significantly between species, season and their interaction. *Vachellia mellifera*, *C. alexandri*, and *Z. mucronata* had a higher gas production potential and *C. collinum* had a lower rate of gas production. Chemical composition was poorly correlated to gas production parameters, but there was a moderate to low correlation between ST and rate of gas production. Besides chemical profile and gas kinetics, more work on animal responses is needed to affirm the nutritional characteristics of the leaves.

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Declarations

Conflict of interest Authors have no conflicts of interest to declare that are relevant to the content of this article.

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