# Browse species selection modulates seasonal digestibility impairments in indigenous goats: Searsia lancea preserves protein supply during drought stress

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## Abstract

Two experiments evaluated the palatability, intake, and nutrient digestibility of indigenous browse species *Searsia lancea* (*S. lancea*) and *Celtis africana* (*C. africana*) in Nguni goats across wet and dry seasons. In Experiment 1, ten male Nguni goats (12 ± 1.7 kg wet season; 17 ± 1.8 kg dry season) were offered *S. lancea*, *C. africana*, and their 1:1 mixture (SL:CA) in a cafeteria-style preference trial. During both seasons, goats strongly preferred SL:CA and *S. lancea* over *C. africana* ($P < 0.05$), with preference indices and eating times. Dry season preference for *S. lancea* intensified amid reduced variability. In Experiment 2, twenty male Nguni goats were fed browse-supplemented diets (*S. lancea*, *C. africana*, or SL:CA with *Eragrostis* hay base) or a control diet (*Medicago sativa* hay, fresh vegetables, and concentrates) in a digestibility trial spanning both seasons. Crude protein digestibility declined from 79.4% (control) to 30.3% (*C. africana*) but only to 41.6% for *S. lancea*. Season × treatment interactions were substantial ($\Delta d = 9.02$), with browse switching nutritionally across seasons. Wet-season browse diets provided 47% more digestible carbon than the control. Browse species can supplement Nguni goat diets during wet seasons, but dry season feeding requires protein supplementation (90–120 g/day).

## Introduction

Ruminant production in increasingly restricted spaces in semi-arid regions faces persistent nutritional challenges, particularly during dry seasons, when the quality and availability of herbaceous forage decline substantially (Mthi et al., 2021). Indigenous browse species common across regions could provide valuable alternative feed resources, supplementing protein and maintaining nutrient availability when conventional forages become limiting (Mudau et al., 2022). However, seasonal variations in nutrient composition and plant secondary metabolite (PSM) concentrations influence voluntary intake and nutrient digestibility, constraining browse utility (Singh et al., 2022). This study investigated seasonal effects on intake and digestibility using two indigenous Southern African tree species, *Searsia lancea* (*S. lancea*, 10.8% CP) and *Celtis africana* (*C. africana*, 15.1% CP), as model species for browse common in different localities in arid and semi-arid regions. The study evaluated preferences and palatability when browse species were offered as discrete choices or in combination, assessed species-specific effects on apparent digestibility in goats fed *Eragrostis curvula* (*E. curvula*) hay as a basal diet, and quantified the magnitude of seasonal and species interactions using effect size analysis and Bayesian integration. It is hypothesized that findings will contribute to evidence-based browse management strategies applicable to semi-arid ruminant production systems globally, promoting sustainable utilization of indigenous browse resources in regions facing similar climatic and economic constraints.

## Materials and method

# Study location

The research was carried out at the Agricultural Research Council-Animal Production (ARC-AP) in Irene, located at 25°89.9'23" S, 28°21.5'23" E. The minimum and maximum temperatures in January were 17°C and 28°C, respectively, while in July, they ranged from 5°C to 21°C.

## Experimental design and animals

This study employed a randomized complete block design investigating browse intake and digestibility in Nguni goats. Twenty indigenous male Nguni goats (approximately 12 months old) were purchased from smallholder farmers in the Sekhukhune region of Limpopo Province, approximately 500 km north of Pretoria, South Africa. The same animals were used in both the wet and dry seasons, with body weights of 12 ± 2.0 kg (wet season) and 17 ± 1.7 kg (dry season), corresponding to a 41% increase attributable to natural growth. Sample sizes were determined through a combined approach that considered prior research protocols (Mengistu et al. 2017), available research infrastructure, and ethical principles of animal research. Upon arrival, goats were quarantined, treated for parasites, and adapted to *Eragrostis curvula* hay and commercial pellets for seven days before trials commenced. Animals were individually housed in 1.5 m × 2.5 m pens with a controlled environment (18–26°C, 45–65% humidity) and were cleaned daily.

## Experimental procedures

*Celtis africana* (CA) and *Searsia lancea* (SL) were collected weekly from the Vegetable, Industrial, and Medicinal Plants Institute (ARC-VIMP), South Africa, during the wet (October-February) and dry (May-July) seasons. Experiment 1: The preference and palatability of these two browse species were tested on goats (n = 10) over four days. Browse was offered on separate boards for 30 minutes, and video recordings were analysed for intake and behaviour, resulting in a relative palatability index (RPI). Experiment 2 involved a digestibility trial with goats (n = 20), on four different diets over 30 days, i) *S. lancea* + *E. curvula* hay, ii) *C. africana* + *E. curvula* hay, iii) SL:CA (1:1) + *E. curvula* hay, or iv) control diet (*Medicago sativa*, commercial pellets, vegetables, and *E. curvula* hay) as shown in Table 1. Each goat received more than 3% DM of its body weight daily, with 100 g DM *E. curvula* as baseline. Orts were weighed for nutritional analysis, and total faecal collection was conducted after an adaptation (5 consecutive days) using harness-mounted bags after a seven-day adaptation period. Actual and proportional dry matter intake (ADMI, PDMI), Organic matter intake (OMI), crude protein intake (CPI), and neutral detergent fibre intake (NDFI) were calculated according to NRC (2007).

## Measurements

Dry matter (DM) was determined by oven-drying at 60°C (Method 930.15; AOAC, 2010). Ash was determined by combustion at 550°C (Method 930.05; AOAC, 2010), with organic matter (OM) calculated as DM minus ash. Crude protein (CP; N × 6.25) was determined by the Kjeldahl method (Method 978.04; AOAC, 2005). Carbon was determined using an automated CHNS elemental analyser (Perkin-Elmer 2400 CHN elemental analyzer). Fibre fractions (NDF, ADF, ADL) followed Van Soest et al. (1990). Ether extract (EE) was determined by Soxhlet extraction (Method 920.39; AOAC, 2010). Non-fibre carbohydrates (NFC) were calculated as NFC = 100 - (Ash + CP + EE + NDF), following Weiss et al. (1992). Condensed tannins (CT) and total phenolic compounds (TPC) were quantified spectrophotometrically (Hattas and Julkunen-Tiitto, 2012).

# Statistical analysis

Statistical analyses were performed using Stata 19.5 (StataCorp, College Station, TX, USA). Data were analyzed separately for each season due to anticipated Season × Treatment interactions. Normal distribution of residuals was verified using the Shapiro-Wilk test, and homogeneity of variance was assessed using Levene's test.

Experiment 1: Browse preferences and intake were analyzed within each season using: $Y_{ijk} = \mu + Browse_i + Day_j + Goat_{k(i)} + \varepsilon_{ijk}$

where $Browse_i$ = fixed effect of browse type; $Day_j$ = fixed effect (days 1–4); $Goat_{k(i)}$ = random effect nested within browse.

Experiment 2 - pooled browse analysis: primary analysis comparing browse-based diets (pooled) against the control diet, one-way analysis of variance (ANOVA) was conducted with treatment group (Control vs. Browse) as the fixed effect. The browse group included all animals receiving any browse species (*C. africana*, *R. lancea*, or RL:CA). Effect sizes were quantified using Cohen's d, calculated as the difference between group means divided by the pooled standard deviation (√MSE).

Species-specific analysis: To evaluate differences among individual browse species, one-way ANOVA was conducted with four treatment groups (Control, *C. africana*, *R. lancea*, RL:CA).

Bayesian analysis: For variables showing significant treatment effects in either season, Bayesian analysis integrated evidence across seasons.

Meta-analysis: meta-analytic statistics were calculated to quantify heterogeneity of treatment effects across seasons.

## Results

# Browse preference and palatability (Experiment 1)

The browse intake and feeding behavior results are presented in Table 1. In the wet season, DM intake differed among browse types (P = 0.024), with goats consuming significantly more SL:CA (48.9 g/30 min) and *S. lancea* (49.1 g/30 min) compared to *C. africana* (18.2 g/30 min). High coefficients of variation (45–117%) reflected large individual variation in young goats. Preference indices differed significantly (P = 0.002), with SL:CA (0.40) and *S. lancea* (0.36) preferred over *C. africana* (0.24).

Table 1
Browse intake, preference indices, and feeding behaviour in Nguni goats during wet and dry seasons.

| **Wet season** | | | | | | |
|---|---|---|---|---|---|---|
| **Parameter** | Unit | *C. africana* | *S. lancea* | SL:CA | SEM | P-value |
| DM intake* | g/30 min | 18.2□ (13.2–42.3) | 49.1□□ (42.5–54.9) | 48.9□ (31.9–78.5) | 7.2 | 0.024 |
| Eating time* | seconds | 108.5□ (35.8-245.5) | 447.0□□ (175.2–564.0) | 580.5□ (269.5-764.5) | 65 | 0.008 |
| Eating rate* | g/sec | 0.2 (0.1–0.3) | 0.1 (0.1–0.2) | 0.1 (0.1–0.2) | 0.09 | 0.458 |
| Sniffing time | seconds | 16.9 ± 12.3 | 14.3 ± 9.9 | 20.4 ± 20.8 | 3.5 | 0.682 |
| Preference index | proportion | 0.24□ ± 0.16 | 0.36□□ ± 0.15 | 0.40□ ± 0.10 | 0.03 | 0.002 |
| **Dry season** | | | | | | |
| DM intake* | g/30 min | 18.2□ (13.0-22.5) | 53.1□ (45.0-66.8) | 55.4□ (46.7–64.5) | 3.0 | < 0.001 |
| Eating time* | seconds | 111.5□ (98.5-154.5) | 389.5□ (288.8-460.2) | 433.5□ (338.2–537.0) | 23 | < 0.001 |
| Eating rate* | g/sec | 0.1 (0.1–0.2) | 0.1 (0.1–0.2) | 0.1 (0.1–0.2) | 0.01 | 0.897 |
| Sniffing time | seconds | 10.0□ ± 6.7 | 17.7□ ± 7.8 | 15.5□□ ± 8.6 | 1.8 | 0.009 |
| Preference index | proportion | 0.14□ ± 0.05 | 0.40□ ± 0.07 | 0.45□ ± 0.08 | 0.02 | < 0.001 |

n = 20 observations per browse type per season (10 goats × 2 days)

□□ Medians or means within a row (within season) with different superscripts differ significantly (P < 0.05, Bonferroni-corrected post-hoc tests)

* Variables presented as median (IQR) due to high coefficient of variation (CV > 70%)

Other variables presented as mean ± SD. SEM = standard error of mean.

## Feed chemical composition and browse intake (Experiment 2)

Chemical composition of experimental browse and control feeds is presented in Tables 2 and 6. During the wet season, *C. africana* contained higher CP (14.5% of DM, or 145 g/kg DM) than *S. lancea* (10.4% of DM, or 104 g/kg DM), whereas during the dry season this pattern reversed, with *S. lancea* containing higher CP (11.9% of DM, or 119 g/kg DM) compared to *C. africana* (7.8% of DM, or 78 g/kg DM).

Table 2
Diet composition of control and browse-based diets offered to Nguni goats during wet and dry seasons.

| **Ingredient (g/kg)[2]** | **Wet season[1]** | | | | **Dry season** | | | |
|---|---|---|---|---|---|---|---|---|
| | **Control** | ***C. africana*** | ***S. lancea*** | **SL:CA** | **Control** | ***C. africana*** | ***S. lancea*** | **SL:CA** |
| *Eragrostis curvula* | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |
| *Medicago sativa* | 425 | 0 | 0 | 0 | 425 | 0 | 0 | 0 |
| Apple | 55 | 0 | 0 | 0 | 55 | 0 | 0 | 0 |
| Butternut | 55 | 0 | 0 | 0 | 55 | 0 | 0 | 0 |
| Spinach | 55 | 0 | 0 | 0 | 55 | 0 | 0 | 0 |
| Pellets | 310 | 0 | 0 | 0 | 310 | 0 | 0 | 0 |
| *C. africana* leaves | 0 | 900 | 0 | 450 | 0 | 900 | 0 | 450 |
| *S. lancea* leaves | 0 | 0 | 900 | 450 | 0 | 0 | 900 | 450 |
| **Nutrient conposition[3] (%)** | | | | | | | | |
| Organic matter | 72.2 | 75.4 | 83.4 | 79.4 | 70.7 | 68.8 | 88.2 | 78.5 |
| Ash | 27.8 | 24.6 | 16.6 | 20.6 | 29.3 | 31.2 | 11.8 | 21.5 |
| Crude protein | 17.0 | 13.5 | 9.8 | 11.7 | 17.3 | 7.4 | 10.9 | 9.1 |
| NDF | 34.3 | 27.9 | 30.8 | 29.4 | 31.0 | 28.5 | 29.8 | 29.1 |
| ADF | 22.8 | 15.5 | 19.2 | 17.4 | 18.0 | 15.3 | 18.6 | 17.0 |
| ADL | 2.7 | 2.8 | 2.7 | 2.8 | 2.4 | 2.9 | 2.7 | 2.8 |
| **Secondary plant metabolites[4]** | | | | | | | | |
| CT | 0.1 | 3.7 | 9.9 | 6.8 | 0.1 | 3.6 | 13.6 | 8.6 |
| TPC | 0.2 | 2.3 | 7.3 | 4.8 | 0.1 | 1.8 | 7.2 | 4.5 |

[1]Wet season ranged from October to February; Dry season ranged from May to July

[2]C. *africana = Celtis africana*; *S. lancea - Searsia lancea*; SL:CA = *S. lancea* and *C. africana* mixture; M. sativa = *Medicago sativa;* Control

[3]NDF = neutral detergent fibre; ADF = acid detergent fibre; ADL = acid detergent lignin; CT = condensed tannins; TPC = total phenolic compounds.

## Digestibility coefficients: Pooled browse vs control

The CPD in control animals (79.4 ± 6.7%) was higher than in browse-fed animals (37.4 ± 9.4%), representing a 42 percentage-point reduction (Cohen's d = 5.28, P < 0.001) (Table 3). Carbon digestibility was also lower in browse-fed animals (70.8 ± 9.8% vs. 52.9 ± 7.6%, difference = 17.9 ± 4.4%, d = 2.13, P = 0.001). Season × treatment interactions were substantial for crude protein digestibility (Δd = 3.79) and carbon digestibility (Δd = 2.89).

# Digestible nutrient supply: Pooled browse vs control

The dCP declined from 14.8 ± 1.4 g/day in control animals to 3.0 ± 1.3 g/day in browse-fed animals (difference = 11.8 ± 0.6 g/day, d = 10.79, P < 0.001 (Table 3). The 3.0 g/day supply in browse-fed animals was substantially below the estimated maintenance protein requirement of 40–50 g/day, representing only 6–8% of the requirement. dOM was reduced from 64.4 ± 7.5 g/day to 52.9 ± 7.2 g/day (difference = 11.5 ± 3.7 g/day, d = 1.61, P = 0.007).

Table 3
Apparent digestibility coefficients and digestible nutrient intakes in Nguni goats fed pooled browse and control diets during wet and dry seasons.

| Parameter[1] | Unit | Wet season[2] | | | Dry season | | | Interaction[3] |
|---|---|---|---|---|---|---|---|---|
| | | Browse (Pooled) | Control | P-value | Browse (Pooled) | Control | P -value | Δd |
| **Digestibility coefficients** | | | | | | | | |
| DMD | % | 55.2 ± 8.5 | 63.0 ± 10.3 | 0.129 | 52.2 ± 8.4 | 71.9 ± 9.4 | <0.001 | 1.39 |
| OMD | % | 62.1 ± 11.0 | 65.5 ± 9.4 | 0.585 | 61.1 ± 7.5 | 73.8 ± 8.8 | 0.010 | 1.25 |
| CPD | % | 68.3 ± 4.4 | 76.8 ± 8.0 | 0.072 | 37.4 ± 9.4 | 79.4 ± 6.7 | <0.001 | **3.79** |
| NDFD | % | 28.6 ± 11.3 | 41.0 ± 15.2 | 0.146 | 31.2 ± 7.8 | 46.3 ± 18.3 | 0.092 | 0.67 |
| CD[4] | % | 73.0 ± 4.1 | 68.4 ± 9.1 | 0.180 | 52.9 ± 7.6 | 70.8 ± 9.8 | 0.001 | **2.89** |
| **Digestible nutrient intakes** | | | | | | | | |
| dOM | g/day | 55.5 ± 10.3 | 57.0 ± 8.3 | 0.785 | 52.9 ± 7.2 | 64.4 ± 7.5 | 0.007 | 1.46 |
| dCP | g/day | 13.1 ± 1.5 | 15.3 ± 1.8 | 0.006 | 3.0 ± 1.3 | 14.8 ± 1.4 | <0.001 | **9.02** |
| dNDF | g/day | 15.2 ± 3.4 | 15.5 ± 3.7 | 0.862 | 11.4 ± 3.2 | 14.0 ± 4.6 | 0.244 | 0.66 |
| dC[4] | g/day | 52.4 ± 3.7 | 35.7 ± 5.3 | <0.001 | 37.1 ± 2.9 | 37.6 ± 1.3 | 0.456 | **4.59** |
| n = 12–15 per treatment (Browse pooled from three browse species: *C. africana*, *S. lancea*, and SL:CA mixture) | | | | | | | | |
| [1] DMD = dry matter digestibility; OMD = organic matter digestibility; CPD = crude protein digestibility; NDFD = neutral detergent fibre digestibility; CD = carbon digestibility; dOM = digestible organic matter; dCP = digestible crude protein; dNDF = digestible neutral detergent fibre; dC = digestible carbon | | | | | | | | |
| [2] Wet season ranged from October to February; Dry season ranged from May to July | | | | | | | | |
| [3] Season × Treatment interaction expressed as Δd (difference in Cohen's d between seasons). Bold indicates large interactions (Δd > 2.0). Calculated as: Δd = \|d_dry - d_wet\|. Effect size interpretation: Small (0.2–0.5), Medium (0.5–0.8), Large (0.8–1.5), Very large (≥ 1.5) | | | | | | | | |

[4]Carbon digestibility (CD) and digestible carbon (dC) determined by elemental carbon analysis of feed and faecal samples.

# Bayesian integration across seasons

Bayesian analysis integrating evidence across both seasons indicated very high posterior probability (> 99.9%) that control diets provided superior CPD overall (posterior mean difference = 20.0%, 95% CI: [15.2%, 24.8%]) and greater dCP (7.7 g/day, 95% CI: [6.9, 8.6]) (Table 4). However, large season × treatment interactions ($I^2$ > 95% for most variables) indicated that these overall effects obscured critical seasonal variation, with browse inadequate during dry season but nutritionally adequate during the wet season.

Table 4
Bayesian posterior distributions

| Variable | Prior (Dry Season) | Likelihood (Wet Season) | Posterior Mean | 95% CI | P(Control > Browse) |
|---|---|---|---|---|---|
| **CPD (%)** | 41.9 ± 4.2 | 8.5 ± 3.0 | 20.0 | [15.2, 24.8] | >99.9% |
| **dCP (g/day)** | 11.8 ± 0.6 | 2.2 ± 0.7 | 7.7 | [6.9, 8.6] | >99.9% |
| **dCarb (g/day)** | 0.4 ± 0.6 | -16.7 ± 2.1 | -0.69 | [-1.7, 0.4] | 10.2% |
| **DMD (%)** | 19.8 ± 4.6 | 7.7 ± 4.8 | 14.0 | [7.5, 20.5] | >99.9% |

Bayesian analysis integrated dry-season data (informative prior) with wet-season data (likelihood) to obtain posterior distributions for both seasons.

# Individual browse species performance

Analysis of individual browse species revealed significant species-specific effects during the dry season, particularly for protein-related variables (Table 5). CPD differed markedly among browse species ($F_{3,14}$ = 36.17, P < 0.001), with *S. lancea* diets supporting 41.6 ± 3.6% digestibility compared to 30.3 ± 3.6% for *C. africana* diets. This represents *S. lancea* achieving 37% higher protein digestibility than *C. africana*.

Table 5
Individual browse species performance during the dry season in Nguni goats.

| Parameter[1] | Control | *C. africana* | *S. lancea* | SL:CA | SEM | F-statistic | P-value | Cohen's d[2] |
|---|---|---|---|---|---|---|---|---|
| **Digestibility coefficients (%)** | | | | | | | | |
| DMD | $71.9^{b}$ | $48.9^{a}$ | $55.7^{ab}$ | $51.9^{a}$ | 4.14 | $F_{3,15}$ = 6.69 | 0.004 | 1.74 |
| OMD | 73.8 | 62.1 | 59.5 | 61.6 | 3.84 | $F_{3,15}$ = 3.04 | 0.062 | 0.68 |
| CPD | $79.4^{c}$ | $30.3^{a}$ | $41.6^{b}$ | $40.3^{ab}$ | 3.51 | $F_{3,14}$ = 36.17 | <0.001 | 3.18 |
| NDFD | 46.3 | 32.6 | 33.4 | 27.6 | 7.75 | $F_{3,14}$ = 1.32 | 0.436 | 0.10 |
| CD[3] | $70.8^{b}$ | $50.4^{a}$ | $55.4^{ab}$ | $52.8^{a}$ | 4.21 | $F_{3,15}$ = 5.88 | 0.007 | 1.19 |
| **Digestible nutrient intakes (g/day)** | | | | | | | | |
| dOM | $64.4^{b}$ | $48.8^{a}$ | $56.1^{ab}$ | $53.8^{ab}$ | 3.26 | $F_{3,15}$ = 4.11 | 0.026 | 2.24 |
| dCP | $14.8^{c}$ | $2.1^{a}$ | $4.2^{b}$ | $2.7^{ab}$ | 0.49 | $F_{3,15}$ = 145.7 | <0.001 | 4.45 |
| dNDF | 14.0 | 10.9 | 13.0 | 10.2 | 2.22 | $F_{3,15}$ = 0.42 | 0.744 | 0.95 |
| dC[3] | $37.6^{ab}$ | $33.9^{a}$ | $40.2^{b}$ | $37.4^{ab}$ | 0.48 | $F_{3,15}$ = 28.85 | <0.001 | 13.13 |

n = 4–5 per treatment (varies by variable due to occasional missing observations)

[1]DMD = dry matter digestibility; OMD = organic matter digestibility; CPD = crude protein digestibility; NDFD = neutral detergent fibre digestibility; CD = carbon digestibility; dOM = digestible organic matter; dCP = digestible crude protein; dNDF = digestible neutral detergent fibre; dC = digestible carbon

[2]Cohen's d effect size for *S. lancea* vs *C. africana* comparison. Effect size interpretation: Small (0.2–0.5), Medium (0.5–0.8), Large (0.8–1.5), Very large (1.5-3.0), Extremely large (> 3.0)

[3]Carbon digestibility and digestible carbon determined by elemental carbon analysis of feed and faecal samples. These parameters serve as proxy measures of digestible organic matter and available energy from all organic sources

[abc]Within rows, means with different superscripts differ significantly (P < 0.05, Bonferroni-corrected pairwise comparisons)

Fibre fractions showed relatively consistent patterns across seasons (Table 6). Non-fibre carbohydrate (NFC) content was numerically higher in *S. lancea* (51.9–53.4% DM) compared to *C. africana* (42.0-43.1% DM) and *M. sativa* (29.2–35.1% DM) across both seasons. During the dry season, *S. lancea* contained 15.1% CT compared to 3.6% CT in *C. africana*. TPC concentrations followed similar patterns, with *S. lancea* containing 7.5–8.1% TPC compared to 2.0-2.6% TPC in *C. Africana* (P < 0.001).

Table 6
Chemical composition of browse species and *Medicago sativa* fed to Nguni goats during wet and dry seasons.

| Parameter[1] | Unit | Wet season[2] | | | | | | Dry season | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *C. africana* | *S. lancea* | SL:CA | *M. sativa* | SEM | P-value | *C. africana* | *S. lancea* | SL:CA | *M. sativa* | SEM | P-value |
| **DM** | % | 86.4$^{a}$ | 87.9$^{a}$ | 87.6$^{a}$ | 95.6$^{b}$ | 0.83 | 0.020 | 88.3$^{a}$ | 93.9$^{b}$ | 92.5$^{ab}$ | 95.5$^{b}$ | 0.91 | 0.005 |
| **OM** | % of DM | 71.0$^{a}$ | 82.4$^{b}$ | 76.7$^{ab}$ | 84.5$^{b}$ | 0.88 | < 0.001 | 66.4$^{a}$ | 87.9$^{c}$ | 78.9$^{b}$ | 85.7$^{bc}$ | 1.31 | < 0.001 |
| **CP** | % of DM | 14.5$^{b}$ | 10.4$^{a}$ | 10.9$^{ab}$ | 20.3$^{c}$ | 0.79 | < 0.001 | 7.8$^{a}$ | 11.9$^{c}$ | 9.4$^{b}$ | 22.9$^{d}$ | 0.25 | < 0.001 |
| **EE** | % of DM | 5.4$^{b}$ | 6.3$^{b}$ | 5.9$^{b}$ | 2.5$^{a}$ | 0.13 | < 0.001 | 3.0$^{b}$ | 3.5$^{b}$ | 3.3$^{b}$ | 1.5$^{a}$ | 0.14 | < 0.001 |
| **NDF** | % of DM | 22.7$^{a}$ | 26.0$^{a}$ | 23.9$^{a}$ | 36.9$^{b}$ | 1.56 | < 0.001 | 24.1$^{a}$ | 25.4$^{ab}$ | 24.3$^{a}$ | 30.7$^{b}$ | 0.99 | 0.029 |
| **ADF** | % of DM | 12.8$^{a}$ | 16.9$^{b}$ | 14.6$^{ab}$ | 27.9$^{c}$ | 1.34 | < 0.001 | 13.2$^{a}$ | 16.9$^{b}$ | 15.5$^{ab}$ | 22.2$^{c}$ | 0.73 | < 0.001 |
| **ADL** | % of DM | 2.9$^{a}$ | 2.8$^{a}$ | 2.8$^{a}$ | 4.2$^{b}$ | 0.18 | 0.001 | 3.1 | 2.8 | 3.3 | 3.2 | 0.17 | 0.983 |
| **NFC[3]** | % of DM | 42.0 | 51.9 | 48.3 | 29.2 | - | - | 43.1 | 53.4 | 49.4 | 35.1 | - | - |
| **Secondary plant metabolites[4]** | | | | | | | | | | | | | |
| **CT** | % of DM | 4.1$^{b}$ | 10.6$^{c}$ | 6.0$^{bc}$ | 0.3$^{a}$ | 0.45 | < 0.001 | 3.6$^{b}$ | 15.1$^{c}$ | 10.7$^{c}$ | 0.2$^{a}$ | 0.53 | < 0.001 |
| **TPC** | % of DM | 2.6$^{b}$ | 8.1$^{d}$ | 4.5$^{c}$ | 0.4$^{a}$ | 0.33 | < 0.001 | 2.0$^{b}$ | 7.5$^{d}$ | 6.2$^{c}$ | 0.3$^{a}$ | 0.45 | < 0.001 |
| n = 3 per treatment | | | | | | | | | | | | | |

[1]DM = Dry matter; OM = Organic Matter; CP = Crude Protein; EE = Ether Extract; NDF = Neutral Detergent Fibre; ADF = Acid Detergent Fibre; ADL = Acid Detergent Lignin; Non-NFC = Fibre Carbohydrates; CT = Condensed Tannins; TPC = Total Phenolic Compounds.

[2] *C. africana = Celtis africana*; *S. lancea = Searsia lancea*; SL:CA = *S. lancea* and *C. africana* 1:1 mixture; *M. sativa = Medicago sativa* (lucerne)

[3]NFC (non-fibre carbohydrates) calculated as: NFC = 100 - (Ash + CP + EE + NDF) according to Weiss et al. (1992).

[4]Secondary plant metabolites (CT and TPC) occur in both fibre-bound and soluble fractions and are reported separately as anti-nutritional indicators and do not contribute to the 100% DM mass balance.

[ab]Means within a row (within season) with different superscripts differ significantly (P < 0.05, Bonferroni post-hoc test).

## Discussion

The goats on *C. africana* diet exhibited lower OM, implying higher ash compared to *S. lancea*. *Celtis africana* demonstrated greater seasonal variation in CP, while *S. lancea* remained relatively stable, suggesting that the browse species could complement each other in mixed-browse systems during the dry season. Although both browses generally met the minimum CP requirements for ruminant maintenance (7–8% DM; Thamina et al., 2020), dry-season *C. africana* was insufficient. Fibre analysis showed comparable NDF levels (22–26% DM) among the browse species during both seasons, which, however, were substantially lower than *E. curvula* hay (> 70% NDF).

*S. lancea* consistently exhibited two to four times higher CT and TPC than *C. africana* during the dry season. These differences reflect distinct evolutionary strategies between evergreen (*S. lancea*) and semi-deciduous (*C. africana*) browse species (Ahmed et al., 2017). Goats demonstrated consistent preference for *S. lancea* and SL:CA over *C. africana* in both seasons, despite *S. lancea* containing CT levels (11–15% DM) that typically reduce palatability (Nsahlai et al., 2011). This preference persisted even when *C. africana* offered higher crude protein (14.5% vs 10.4% in the wet season), indicating that protein content alone does not determine browse selection in Nguni goats. High individual variability in young goats (CVs 45–117%) reflected heterogeneity in browse acceptance, likely related to differences in tannin tolerance (Silanikove, 2000). This variability decreased substantially in older animals (CVs 26–36%), consistent with preference learning and rumen microbial adaptation. Importantly, *S. lancea* provided 100% more digestible protein than *C. africana* (4.2 vs 2.1 g/day), suggesting that goats may possess evolved mechanisms for detecting superior browse species even in the presence of elevated secondary metabolites. The *S. lancea's* superior performance, particularly its ability to preserve protein digestibility at 37% above *C. africana* levels (41.6% vs 30.3%) and double the digestible protein supply, suggests fundamental biochemical differences between these browse species that warrant further investigation. *S. lancea*'s superior protein digestibility despite 4-fold higher tannin concentrations (15.1% vs 3.6%) suggests that tannin structure, rather than concentration, determines nutritional outcomes. *Searsia lancea's* ability to provide more digestible carbon than the control diet, even during the dry season, suggests either a higher non-structural carbohydrate content or lower fibre-bound energy. This compensatory mechanism may partially offset protein deficits and explain why *S. lancea*-fed animals, despite receiving only 4.2 g digestible protein daily, showed less severe weight loss than *C. africana*-fed animals. The 27–41% depression in CPD observed for browse diets during the dry season corresponds to the elevated CT concentrations. *S. lancea's* dry-season CT level of 15.1% DM exceeded the 10–12% threshold at which irreversible tannin-protein complexes form, rendering dietary protein unavailable for both ruminal fermentation and post-ruminal digestion. However, the 37% better CPD in *S. lancea* compared to *C. africana* suggests that factors beyond simple tannin concentration, potentially tannin structure, protein characteristics, or compensatory nutrients influence nutritional outcomes. The substantial reduction in voluntary intake observed with browse-based diets during the dry season (ADMI 387–435 g/day, representing 2.1–2.8% of body weight) indicates a critical nutritional constraint beyond digestibility limitations. The resulting weight loss (-0.05 to -0.08 kg/day ADG) during the dry season suggests that intake limitations, constrained performance. Smallholder farmers may strategically plant or selectively harvest *S. lancea* over *C. africana*, and decrease supplement requirements by an estimated 25–50 g/day of protein concentrate to curb dry season weight loss. During the wet season, browse-fed animals consumed 47% more digestible carbohydrate than control animals (52.4 vs 35.7 g/day), effectively reversing the dry season energy deficit. This massive interaction ($\Delta d = 4.59$) demonstrates that browse is not uniformly inferior to concentrate-based diets. Rather, its nutritional value is profoundly season-dependent.

## Declarations

**Statement of animal rights**

This study was approved by the Animal Ethics Committee of the ARC-AP (Ref: APIEC18/14) and the Animal Research Ethics Committee of the University of South Africa (Ref no. 2019/CAES/072).

Conflict of Interest

No conflict of interest.

**Data and model availability statement**

None of the data was deposited in an official repository. Data can be made available from the author upon request

Author Contributions

France Phiri: conceptualization, methodology, investigation, formal analysis, data curation, writing - original draft preparation. Arnold Tapera Kanengoni: conceptualization, supervision, validation, writing - review & editing. Dawood Hattas: methodology, validation, formal analysis.

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