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Effect of shoot morphology on browse selection by free ranging goats in a semi-arid savanna

A. Sebata [a,*], L.R. Ndlovu [b]

[a] Department of Forest Resources & Wildlife Management, National University of Science & Technology (NUST), P.O. Box AC 939, Ascot, Bulawayo, Zimbabwe
[b] Vice-Chancellor's office, National University of Science & Technology (NUST), P.O. Box AC 939, Ascot, Bulawayo, Zimbabwe

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ABSTRACT

Woody plants protect themselves against loss of valuable nutrients and photosynthetic tissue to herbivores. Plant anti-herbivory defences influence their selection by browsers. Woody plant species which produce new leaves on old lignified branches (shoot-limited, SL) (*e.g.*, *Terminalia prunioides* and *Commiphora pyracanthoides*) have different anti-herbivory mechanisms to those that produce new leaves on new growing shoots (shoot-dominated, SD) (*e.g.*, *Grewia tenax*, *Grewia monticola* and *Colophospermum mopane*). Shoots and leaves of SD species are more exposed to herbivores than SL species requiring better chemical defences in the form of high fibre and condensed tannins (CT) (proanthocyanidins) contents. We studied selection patterns of Matebele goats browsing on *T. prunioides* and *C. pyracanthoides* (SL species) and *G. tenax*, *G. monticola* and *C. mopane* (SD species) in an open savanna during the plant growth season (November to May). Browse selection was then related to crude protein (CP), neutral detergent fibre (NDF), acid detergent fibre (ADF), condensed tannins (CT), total phenolics (TP), *in vitro* gas production (IVGP) and *in vitro* dry matter digestibility (IVDMD). The two SL species (*T. prunioides* and *C. pyracanthoides*) had higher browse selection indices (BSI) (1.96 *vs* 0.37) than the three SD species (*G. monticola*, *G. tenax* and *C. mopane*). The SD species had higher NDF (553.25 *vs* 410.95 g/kg DM), ADF (353.53 *vs* 238.49 g/kg DM) and CT (15.87 *vs* 0.43 g/kg DM) than SL species. The SL species had higher IVGP after 48 h (68.99 *vs* 33.00 ml/300 mg DM) and IVDMD (0.54 *vs* 0.43) than SD species. *T. prunioides* was the most fermentable and *C. pyracanthoides* the most digestible while *C. mopane* had the lowest IVGP and IVDMD. Browse selection indices had inverse relationships with NDF ($r=-0.92$, $P<0.01$), ADF ($r=-0.91$, $P<0.01$) and CT ($r=-0.87$, $P<0.01$) and positive relationships with IVGP ($r=0.97$, $P<0.01$) and IVDMD ($r=0.68$, $P<0.05$). We conclude that SL species had higher BSI than SD species due to their lower contents of CT, NDF and ADF and higher digestibility and rumen fermentation. The higher NDF, ADF and CT in SD species were an anti-herbivory defence strategy.

1. Introduction

Goats in semi-arid south-western Zimbabwe rely on woody species for their nutrition. They utilise browse from different woody species to satisfy their needs for nutrients (Papachristou et al., 1999; Ramirez et al., 1991), with chemical and physical properties of the plants acting as browsing deterrents (Bryant et al., 1991; Cooper and Owen-Smith, 1986; Van Soest, 1994). Determining browse selection is an

Abbreviations: ADF, acid detergent fibre; AOAC, Association of Official Analytical Chemists; BSI, browse selection index; CP, crude protein; CT, condensed tannins; DM, dry matter; IVDMD, *in vitro* dry matter digestibility; IVGP, *in vitro* gas production; NDF, neutral detergent fibre; SD, shoot-dominated; SL, shoot-limited; TP, total phenolics.

* Corresponding author. Tel.: +263 9 282842; fax: +263 9 286803.
E-mail address: asebata1554@nust.ac.zw (A. Sebata).

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important prerequisite for assessing the impacts of browsers on their environments and understanding plant–herbivore interactions (Tanentzap et al., 2009). Factors that drive browse selection are complex and remain poorly understood, although it has long been assumed that animals select diets that optimise nutrient intake and minimise intake of anti-nutrients (Atwood et al., 2001; Behmer et al., 2002). Plants need to protect themselves against loss of valuable nutrients and photosynthetic tissue to herbivores (Rosenthal and Janzen, 1979).

Scogings et al. (2004) divided woody plants into two groups *viz.* those that produce all their new leaves on new long shoots (shoot-dominated species, SD) and those that produce most of their new leaves in clusters on short shoots at the nodes of old unbrowsable branches (shoot-limited species, SL). Shoot-dominated species depend on active apical buds to extend internodes and add new leaf area and should thus have higher concentrations of nutrients than SL species which simply add new leaf area without shoot elongation (Ganqa and Scogings, 2007; Scogings et al., 2004). Rhoades (1979) suggested that SD species are more valuable and therefore vulnerable to herbivores than SL species, requiring mechanisms of avoiding herbivory.

Plant anti-herbivory defence includes high fibre content (Jung and Allen, 1995; Shipley and Spalinger, 1992), high condensed tannins (CT) (proanthocyanidins) levels (Cooper and Owen-Smith, 1985) and physical deterrents (Dziba et al., 2003). In arid and semi-arid regions fibre and condensed tannins represent a basic mechanism for plant competitiveness and are an important adaptation to harsh, resource limited environments (Freeland, 1991). Shoots and leaves of SD species are more exposed to herbivores than SL species (Rhoades, 1979; Scogings et al., 2004). Plants and plant parts exposed to herbivores are expected to be better chemically defended than those protected by physical deterrents (Cooper and Owen-Smith, 1985). Shoot-dominated species are thus predicted to have higher fibre and CT contents than SL species which have physical deterrents in the form of spines and thorns at similar leaf phenophases. However, browsers such as goats are able to use their mobile upper lips to crop shoots and leaves protected by thorns and spines. Shoot-limited species also rapidly replace lost tissues through regrowth (Scogings et al., 2004). For proper management of rangelands, the influence of shoot morphology on herbivore browsing patterns needs to be understood.

Woody species with low concentrations of crude protein provide inadequate amounts of nitrogen for rumen microbial activity and will therefore be less acceptable to browsers (Augner, 1995; Lundberg and Astrom, 1990), while high levels of CT and fibre will reduce browse digestibility (Crawley, 1983). Condensed tannins further reduce protein availability for absorption by limiting ruminal microbial growth and lowering the fractional absorption of amino acids from the intestine (Waghorn, 2008).

Browse that is highly fermentable with high digestibility results in high nutrient availability. Sandoval-Castro et al. (2005) suggested that goats were able to select browse with high digestibility. Digestibility is a measure of energy value and hence quality of browse (Coates and Mayer, 2009). Browse that is readily fermentable provides nutrients to rumen microorganisms (Umunna et al., 1995) which in turn increases the rate of the fermentation process. Thus, rumen fermentation and digestibility of woody species are expected to influence browse selection.

In semi-arid south-western Zimbabwe rainfall is low and erratic resulting in plant growth occurring over short periods of less than five months (Sebata and Ndlovu, 2010). The onset of rains triggers shoot and leaf sprouting while the length of the rainy season will determine the duration of the growth period in woody species under arid and semi-arid conditions (Shackleton, 1999). Goats therefore need to maximise nutrient intake during the short plant growth period to be able to build enough body reserves for later mobilisation during the dry period when feed is scarce. Shoot and leaf maturity is expected to affect nutrient availability to the foraging goats. Crude protein (CP) content declines while fibre increases as leaves mature during the growth season (Cooper et al., 1988; Scogings et al., 2004).

The objective of this study was to determine the selection patterns of Matebele goats browsing on *Terminalia prunioides* and *Commiphora pyracanthoides* (SL species), *Grewia tenax*, *Grewia monticola* and *Colophospermum mopane* (SD species) in an open savanna during the plant growth season (November to May). Browse selection was then related to crude protein (CP), neutral detergent fibre (NDF), acid detergent fibre (ADF), condensed tannins (CT) and total phenolics (TP), *in vitro* gas production (IVGP) and *in vitro* dry matter digestibility (IVDMD). We tested the following hypotheses: 1) SD and SL species are selected similarly 2) SD and SL species have similar CP, NDF, ADF, CT, TP, IVGP and IVDMD contents.

2. Materials and methods

2.1. Study site description

The study was carried out at Kwalu Communal lands (21°25′S, 29°30′E, altitude 1150 m a.s.l.), which are 415 km^2 in size and 87 km northwest of Beitbridge town, Zimbabwe. Mean annual rainfall recorded over the last 30 years was 332.9 mm (range: 83–527), with most of it falling during a single rainy season between November and April. Mean monthly temperature ranges from 7.9 °C to 33.6 °C, with July recording the lowest and January the highest. The rainfall and mean temperature records for the 2006/2007 rainy season are shown in Fig. 1. The area is dry with a relative humidity of between 48% and 61% and a negative moisture balance.

The vegetation comprises a short, shrubby structure that varies from open to closed woodland (Timberlake and Mapaure, 1999). The major woody species are *T. prunioides*, *C. pyracanthoides*, *G. monticola*, *G. tenax* and *C. mopane*. The herbaceous layer includes the gramenoid species; *Eragrostis rigidior*, *Panicum maximum*, *Panicum coloratum* and *Urochloa mosambicensis* and various forb species.

2.2. Experimental goats and their management

The Matebele goats are small-framed with a characteristic mixture of colour patterns throughout the body and are well adapted to the harsh conditions of the semi-arid south-western Zimbabwe (Sibanda et al., 2000). Goats belonging to five households were used in this study. The five households were systematically selected from 52 households in