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Forage quality, twig diameter, and growth habit of woody plants browsed by black rhinoceros in semi-arid subtropical thicket, South Africa

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Abstract

Rapid growth of the black rhino (*Diceros bicornis*) population in the Great Fish River Reserve (GFRR), South Africa, has potential to negatively impact the semi-arid thicket vegetation that occurs in the reserve. Woody plants presenting nutritious twigs to twig-biting browsers are assumed to be potentially at greater risk of losing biomass than those that do not and should be considered in management protocols. We investigated plant growth habits, twig diameter and forage quality of woody species commonly browsed by black rhino in the GFRR to see if any fit a high risk profile. Samples of twigs 2, 6, 10 and 14 mm in diameter, and the leaves thereon, were collected during the wet season to determine the dry mass (DM), crude protein (CP) and neutral detergent fibre (NDF) concentrations of leaves and wood, as well as leaf:stem ratios (LSR). CP and LSR decreased while NDF and DM increased with twig diameter. Rates of change appeared to be greater for evergreen than deciduous species. Black rhinos foraging in the GFRR are therefore expected to inflict greatest biomass losses on deciduous species, especially ones with many long shoots. We recommend that relationships among forage quality and growth habits of woody species need to be better understood for the management of black rhinos in semi-arid subtropical thicket.
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1. Introduction

The semi-arid vegetation of the Thicket Biome in South Africa is known to be susceptible to mammal herbivory (Low and Rebelo, 1998; Midgley et al., 1997). The Great Fish River Reserve (GFRR) covers $450 \, km^2$ in the Thicket Biome and has a population of black rhinoceros (*Diceros bicornis*) (black rhino) that is among 17 rated as "important" worldwide (Emslie and Brooks, 1999). The rapid growth of the black rhino population since the founder group was introduced during 1986 raises concerns about their potential negative impacts on the semi-arid vegetation in the GFRR. Because the impacts of herbivores on vegetation feed back to the herbivore community, black rhino feeding behaviour could also lead to potential negative effects on other, smaller herbivores (Danell et al., 1985; Gordon, 2000; Wilson and Kerley, 2003). To manage changes in the vegetation of GFRR, rhino populations will need to be manipulated according to appropriate protocols developed from better understanding of the vegetation–herbivore interaction at the level of the individual plant through to higher levels of biological organisation (Gordon, 2000).

Feeding ecology has been identified as a priority area of research in black rhino conservation because of its importance for estimating optimal stocking rates for wild populations and improving the productivity of captive animals through improved nutrition (Emslie and Brooks, 1999). Diet selection by mammal browsers is not only influenced by their ability to select plant species from a diverse assemblage of species, but is also influenced by their ability to select from an array of plant parts within individual plants (Palo et al., 1992; Vivås et al., 1991). Mammal herbivores thus feed from a wide range of plant tissues that differ in chemical/physical determinants of their forage value (Danell et al., 1985; Illius et al., 1999; Villalba and Provenza, 1999). Like other mammal herbivores, black rhinos are known also to compile their diets according to various characteristics of plants and plant parts (Ganqa et al., 2005; Muya and Oguge, 2000; Oloo et al., 1994;). For browsers that ingest much of their diet by biting twigs (including leaves), such as black rhino, variations in forage quality among twigs of different diameters are likely to be important in determining their foraging efficiency (e.g., rate of energy intake) and therefore their reproductive success (Kotze and Zacharias, 1993; Shipley et al., 1999). This is because correlations between forage quality and twig size compel browsers to compromise between nutrient intake and dry matter intake (Shipley et al., 1999).

While the effects of twig size on potential bite quality have been studied in boreal and temperate systems, they have not been studied in as much detail in semi-arid subtropical systems (Wilson and Kerley, 2003). For birch trees (*Betula* spp.) browsed by moose (*Alces alces*) in boreal forests, nitrogen concentration and digestibility are negatively related to twig diameter, while fibre concentration is positively related to twig diameter (Palo et al., 1992). Similar relationships between forage quality and twig size have been found among a range of xeric thicket species at Addo Elephant National Park (Wilson and Kerley, 2003). The twig-biting browser must therefore choose between either nutrient intake maximisation and restricted dry matter intake at small twig diameters, or dry matter intake maximisation and reduced digestibility at large twig diameters (Palo et al., 1992; Shipley et al., 1999; Vivås et al., 1991).

Among the effects that the feeding behaviour of herbivores has on vegetation is the effect on biomass (Gordon, 2000). The impact of large browsers on individual plants, populations and communities is affected by how much biomass is removed by twig

selection (Shipley et al., 1999; Vivås et al., 1991). Woody plants that present browsable twigs to a twig-biting browser are potentially at risk of losing proportionally more biomass than plants that do not present browsable twigs to the same herbivore (Shipley et al., 1998), especially if the twigs are of high nutritional value as forage. Management of large browsers in areas inhabited by plants with such characteristics would need to include specific monitoring of those species.

Variations in the forage quality of woody plants in Africa have been largely explained in terms of resource-driven (RD) hypotheses, especially the carbon/nutrient balance (CNB) and growth rate (GR) hypotheses (Bryant et al., 1991; Coley, 1988), although they have not been adequately tested in subtropical systems (Naiman et al., 2003; Scholes, 1997). According to these hypotheses, developed in boreal and tropical forests, forage quality is expected to be lower in evergreen species than in deciduous species (Coley and Aide, 1991; Herms and Mattson, 1992). Evergreen species are generally assumed to be slower growing than deciduous species and therefore they are expected to allocate proportionally more resources to storage, maintenance and defence (Bryant et al., 1992; Tuomi et al., 1988).

Knowledge of the variation in quality within and among woody plants in relation to mammal browsers in semi-arid subtropical systems is scarce (Scogings, 2003). Furthermore, observations in semi-arid subtropical savannas of southern Africa and southern Texas contradict the assumptions of the above mentioned models (Nelson et al., 2002; Rooke et al., 2004; Scogings et al., 2004). For example, canopy retention does not generally correlate with growth rate and N concentration in semi-arid savannas. Therefore, it is clear that the existing hypotheses are not sufficiently developed to allow confident predictions to be made of variations in forage quality in semi-arid subtropics, and therefore there is effectively no substantive theoretical framework for predicting the quality of woody plants for thicket browsers. Significantly more basic research is required that would contribute to the existing knowledge base. As a result, the improved understanding of browse–browser interactions in semi-arid subtropical systems would guide the development of management-oriented models for black rhino conservation in thicket vegetation.

Because the conventional hypotheses have been found to fall short in semi-arid subtropical savannas, and in an effort to improve understanding, it has been postulated that the leaves of species producing all their new leaves on new long shoots have higher concentrations of cell wall components than the leaves of species that produce most of their new leaves in clusters on short shoots (Scogings et al., 2004). The reason given for the pattern of fibre concentrations predicted by the aforementioned "shoot morphology" hypothesis is that, in terms of the optimal defence hypothesis (Rhoades, 1979), the leaves of long-shoot (LS) species, which add new leaf area by extending internodes are more vulnerable to browsing than those of short-shoot (SS) species, which simply add new leaf area without shoot elongation. Increased cell wall concentrations would make the leaves tougher for a herbivore.

A mechanistic explanation for higher cell wall concentrations in the leaves of LS species is that fibre demand increases when nutrient demand increases (Matsuki, 1996; Weaver and Herrmann, 1997). Because active meristematic tissues have high concentrations of nutrients (Herms and Mattson, 1992), species that depend on active apical buds for leaf production may be expected to have higher concentrations of both nutrients and fibre than species that do otherwise. Furthermore, competition for nutrients among shoot apices and leaves increases the C:N ratio in leaves (Honkanen et al., 1994; Senn and Haukioja, 1994),

allowing excess C to be available for cell walls of LS species. The "shoot morphology" model is therefore a hypothesis that attempts to integrate resources and herbivores as driving factors determining the expression of forage quality characteristics among woody species in semi-arid, subtropical areas (Scogings et al., 2004).

The objective of this study was to investigate variations in (1) crude protein (CP) and neutral detergent fibre (NDF) concentrations, and (2) biomass allocation to leaves and stems at two levels of organisation of the forage resource used by black rhinos in the GFRR. Variations were studied among five woody species that are browsed by black rhinos and vary in canopy retention and shoot morphology (deciduous vs evergreen, LS vs SS), as well as among different size classes of twigs used by black rhino within species. In doing so, we were able to test whether or not CP decreases while biomass and NDF increase with increasing twig size. Because we studied species varying in growth habits, we were also able to explore whether or not deciduous species have higher CP and lower NDF concentrations than evergreen, and LS species have higher NDF concentrations than SS species. From this information we could assess the extent to which plants browsed by black rhino fit a high risk profile.

2. Methods

The GFRR is in the Eastern Cape Province of South Africa. It covers an area of 45 000 ha and is a complex of three reserves, which are Sam Knott Nature Reserve, Andries Vosloo Kudu Reserve and Double Drift Game Reserve. Double Drift is separated from the other two reserves by the Great Fish River. Fieldwork was conducted in the Andries Vosloo Kudu Reserve, which covers 6 500 ha and is located between 33° 04′ and 33° 09′ S, and 26° 37′ and 26° 49′E, 35 km north-east of Grahamstown.

The altitude varies from 183 to 548 m above sea level. The climate is semi-arid, with mean annual rainfall of 435 mm, varying from approximately 250 mm yr^{-1} at lower altitudes to 500 mm yr^{-1} at higher altitudes (Palmer, 1981). Temperature ranges from summer maxima exceeding 40 °C to winter minima as low as 0 °C (Palmer, 1981). Geologically the area consists predominantly of grey and red mudstone and sandstone (Johnson and Keyser, 1976). The dominant vegetation of the study area is typically succulent or spiny scrub, 2–3 m tall, and occurring in three principal communities: (i) short succulent thicket, (ii) medium succulent thicket, and (iii) bush-clump savanna (Evans et al., 1997).

Together with black rhinos, the study area supports a wide variety of ungulates. The most abundant browser is kudu (*Tragelaphus strepsiceros*), with an estimated stocking rate of 11–16 ha animal^{-1}. Other browsers and mixed feeders include eland (*Taurotragus oryx*), steenbok (*Raphicerus campestris*), springbok (*Antidorcas marsupialis*), grey duiker (*Sylvicapra grimmia*) and bushbuck (*Tragelaphus scriptus*), which are present in smaller numbers.

Five woody species (*Acacia karroo*, *Azima tetracantha*, *Diospyros lycioides*, *Gymnosporia polyacantha* and *Plumbago auriculata*) were sampled during the early wet season (December), to quantify plant factors that could influence diet selection by the rhino. The most frequently browsed plant species in the early wet season is a succulent, *Euphorbia bothae*, which makes up 68.9% of the browsed plants (Ausland et al., 2001). The five species sampled for this study were selected because they are among the most frequently browsed woody species, making up 10.5% of all browsed plants (Ausland et al., 2001).

More importantly, however, they represent various canopy retention patterns (deciduous versus evergreen), physical defences (spinescent versus non-spinescent) and shoot growth patterns (short shoots versus long shoots).

Acacia karroo, *D. lycioides* and *P. auriculata* are deciduous. The spinescent species are *Acacia karroo*, *Azima tetracantha* and *G. polyacantha*, which all have long, straight spines. *Acacia karroo* and *G. polyacantha* produce most of their new leaves in discrete clusters (whorls or tufts) of large primary leaves and small secondary leaves at the nodes of old shoots or branches (Fig. 1). Such an arrangement of leaves is known as heterophylly, which may be characterised by the nodes being raised into short shoots or spurs (Bell, 1991). Conversely, the remaining species produce all their new leaves on new long shoots, which bear one or two leaves per node.

Twigs that were 2, 6, 10 and 14 mm in diameter were collected from three replicates of each species in areas where diet selection was observed. A replicate comprised a number of twigs collected from different plants until there were enough twigs to provide sufficient dry material for chemical analysis. The above mentioned twig diameters were used because 99% of twigs browsed by rhinos in a previous study were 1–10 mm in diameter (Ausland et al., 2001). The range of diameters sampled agrees with that observed elsewhere in the Thicket Biome (Wilson and Kerley, 2003). The samples were oven-dried at 60 °C for three days. The dried leaves and wood were weighed separately and analysed for CP (Tecator 2300 Kjeltec Analyser) and NDF (ANKOM 200/220 Fibre Analyser) according to standard procedures (AOAC, 1984; Goering and van Soest, 1970). Because a number of twigs from different plants made up each replicate, the average dry mass (DM), CP, NDF and leaf: stem ratios (LSR) could be estimated per twig. Wood DM and LSR were square-root transformed, but leaf DM, leaf CP, as well as leaf and wood NDF were not transformed because their values were normally distributed around a mean. Variations in

a   b

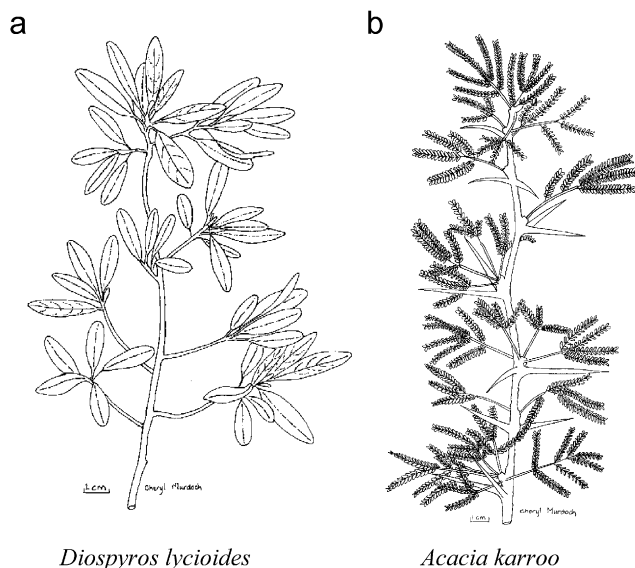*Diospyros lycioides*   *Acacia karroo*

Fig. 1. Examples of (a) long-shoot, *Diospyros lycioides* and (b) short-shoot morphology, *Acacia karroo* (from Scogings et al., 2004).

plant characteristics among replicates, as affected by species and twig diameter, were modelled with standard ANOVA procedures. Within species, relationships between twig diameter and plant factors were modelled with regression analysis.

3. Results

The variation in leaf CP among plant species interacted with twig diameter ($F_{12,40} = 4.43$, $p < 0.001$) (Table 1). At all twig diameters, *G. polyacantha* leaves had the lowest CP, while *P. auriculata* and *Azima tetracantha* leaves generally had the highest. As twig diameter increased, leaf CP decreased the most in *Azima tetracantha* and *G. polyacantha*. The variation in wood CP among plant species was also affected by twig diameter ($F_{12,40} = 3.06$, $p < 0.01$). At 2 and 6 mm diameter, *Azima tetracantha* had the highest wood CP, while at 10 and 14 mm, both *Azima tetracantha* and *P. auriculata* had the highest. At 2 mm, *G. polyacantha* and *Acacia karroo* had the lowest wood CP, but at all other twig diameters, *G. polyacantha* had the lowest (Table 1). Wood CP decreased with increasing diameter the most in *Azima tetracantha* and *D. lycioides*. Generally, CP at all diameters varied a lot among species.

Variations among species in leaf NDF ($F_{12,40} = 2.13$, $p < 0.05$) and wood NDF ($F_{12,40} = 4.30$, $p < 0.001$) were affected by twig diameter (Table 2). While *Azima tetracantha* had the lowest leaf NDF at smaller diameters, both *Azima tetracantha* and *G. polyacantha*

Table 1
Mean crude protein ($\pm$ SE) of leaves and wood of twigs of different diameters for five woody species browsed by black rhinos during the early wet season in the Great Fish River Reserve, South Africa

Plant parts	Plant species	Crude protein (%)			
		2 mm	6 mm	10 mm	14 mm
Leaves	*Acacia karroo*	13.7[b]	13.7[c]	12.4[b]	12.8[b,c]
		(0.11)	(0.13)	(0.38)	(0.24)
	Azima tetracantha	16.2[c]	17.7[e]	16.2[c]	13.9[c]
		(0.26)	(0.50)	(1.13)	(0.25)
	Diospyros lycioides	14.0[b]	12.0[b]	12.1[b]	12.0[b]
		(0.38)	(0.35)	(0.46)	(0.22)
	Gymnosporia polyacantha	9.0[a]	6.9[a]	6.7[a]	6.8[a]
		(0.54)	(0.08)	(0.29)	(0.01)
	Plumbago auriculata	16.4[c]	15.3[d]	17.3[c]	17.4[d]
		(0.50)	(0.31)	(1.11)	(0.98)
Wood	*Acacia karroo*	6.1[a]	5.7[c]	4.4[a,b]	4.3[b]
		(0.65)	(0.13)	(0.23)	(0.09)
	Azima tetracantha	10.2[d]	8.7[d]	6.4[c]	5.5[c]
		(0.28)	(0.66)	(0.56)	(0.40)
	Diospyros lycioides	7.6[b]	6.6[c]	4.6[b]	3.9[a,b]
		(0.28)	(0.53)	(0.20)	(0.17)
	Gymnosporia polyacantha	6.3[a]	3.8[a]	3.4[a]	3.3[a]
		(0.37)	(0.04)	(0.22)	(0.02)
	Plumbago auriculata	8.8[c]	6.4[c]	6.1[c]	6.5[c]
		(0.52)	(0.16)	(0.71)	(0.37)

Superscript letters indicate significant differences among plant species according to the least significant difference ($n = 3$; $p < 0.05$).

Table 2

Mean neutral detergent fibre ($\pm$SE) of leaves and wood of twigs of different diameters for five woody species browsed by black rhinos during the early wet season in the Great Fish River Reserve, South Africa

Plant parts	Plant species	Neutral detergent fibre (%)			
		2 mm	6 mm	10 mm	14 mm
Leaves	*Acacia karroo*	40.5[b]	49.0[b]	50.2[b]	46.8[b]
		(0.73)	(3.16)	(1.97)	(1.30)
	Azima tetracantha	28.7[a]	22.2[a]	40.9[a]	33.5[a]
		(0.90)	(8.60)	(0.67)	(1.49)
	Diospyros lycioides	50.9[c]	53.5[c]	60.0[c]	53.2[b]
		(0.14)	(2.47)	(0.62)	(0.36)
	Gymnosporia polyacantha	40.4[b]	41.6[b]	40.9[a]	38.2[a]
		(0.96)	(1.45)	(0.46)	(0.57)
	Plumbago auriculata	52.7[c]	52.7[c]	52.0[b]	48.6[b]
		(1.94)	(3.10)	(4.00)	(4.47)
Wood	*Acacia karroo*	63.5[c]	66.3[b]	70.5[b]	72.7[a]
		(3.31)	(0.59)	(0.63)	(1.03)
	Azima tetracantha	49.5[a]	63.5[a,b]	65.8[a]	75.8[a]
		(0.65)	(1.14)	(1.78)	(0.34)
	Diospyros lycioides	59.0[b]	60.0[a]	64.7[a]	72.9[a]
		(0.57)	(1.33)	(1.10)	(1.43)
	Gymnosporia polyacantha	58.5[b]	70.2[c]	73.6[b]	79.3[b]
		(2.35)	(1.73)	(0.89)	(1.24)
	Plumbago auriculata	64.3[c]	70.6[c]	73.0[b]	78.6[b]
		(0.47)	(2.41)	(1.46)	(1.82)

Superscript letters indicate significant differences among plant species according to the least significant difference ($n = 3$; $p < 0.05$).

were lowest at larger diameters. At smaller diameters, both *D. lycioides* and *P. auriculata* had the highest leaf NDF, but at 14 mm diameter, *Acacia karroo*, *D. lycioides* and *P. auriculata* had the highest leaf NDF. At 2 mm diameter, *Azima tetracantha* had the lowest wood NDF, but at 14 mm diameter, the lowest wood NDF was found in *Acacia karroo*, *Azima tetracantha* and *D. lycioides* (Table 2). At 2 mm diameter, *Acacia karroo* and *P. auriculata* had the highest wood NDF, but at 14 mm diameter, the highest was found in *G. polyacantha* and *P. auriculata*. Wood NDF increased with twig diameter mostly in *Azima tetracantha* and *G. polyacantha*. Generally, the variation in NDF among species increased with increasing twig diameter.

Leaf DM for the smaller twigs did not vary across species, but did vary for the larger twig diameters ($F_{12,40} = 2.77$, $p < 0.008$) (Table 3). At 10 mm diameter, *Acacia karroo* and *Azima tetracantha* had less leaf DM than *G. polyacantha* and *P. auriculata* had, but at 14 mm diameter they had the same. Likewise, wood DM for the smaller twigs did not vary across species, but did vary for the larger twig diameters ($F_{12,40} = 11.27$, $p < 0.001$). For both 10 and 14 mm twigs, *P. auriculata* had the highest wood DM.

LSR also varied among plant species according to twig diameter ($F_{12,40} = 14.45$, $p < 0.001$) (Table 4). As twig diameter increased, the differences among species became less. At 2 mm diameter, LSR was lowest for *G. polyacantha*, and highest for *P. auriculata* and *D. lycioides*. At 6 mm, LSR was lowest for *Azima tetracantha* and *P. auriculata*, but highest

Table 3
Mean dry mass ($\pm$SE) of leaves and wood of twigs of different diameters for five woody species browsed by black rhinos during the early wet season in the Great Fish River Reserve, South Africa

Plant parts	Plant species	Dry mass (g)			
		2 mm	6 mm	10 mm	14 mm
Leaves	*Acacia karroo*	0.6	4.6	8.6[a]	29.4[b]
		(0.02)	(0.59)	(2.28)	(5.28)
	Azima tetracantha	0.7	2.9	7.9[a]	34.4[b]
		(0.06)	(0.15)	(2.16)	(5.95)
	Diospyros lycioides	1.0	6.2	14.4[b]	19.3[a]
		(0.04)	(1.19)	(2.99)	(2.91)
	Gymnosporia polyacantha	0.2	4.6	22.9[c]	26.9[b]
		(0.02)	(0.65)	(2.3)	(4.86)
	Plumbago auriculata	0.5	2.4	20.9[c]	29.3[b]
		(0.06)	(0.48)	(2.41)	(5.89)
Wood	*Acacia karroo*	0.6	8.5	31.1[a]	116.0[a]
		(0.01)	(1.38)	(5.88)	(13.2)
	Azima tetracantha	0.7	9.7	39.3[a]	160.3[b]
		(0.01)	(1.03)	(0.19)	(11.37)
	Diospyros lycioides	0.7	7.9	32.2[a]	64.3[c]
		(0.01)	(0.65)	(6.00)	(18.02)
	Gymnosporia polyacantha	0.4	11.4	62.5[b]	132.4[a]
		(0.04)	(0.86)	(9.81)	(12.38)
	Plumbago auriculata	0.4	9.8	101.3[c]	203.8[d]
		(0.07)	(1.23)	(15.3)	(18.02)

Superscript letters indicate significant differences among plant species according to the least significant difference ($n = 3$; $p < 0.05$).

Table 4
Mean leaf:stem ratio ($\pm$SE) of twigs of different diameters for five woody species browsed by black rhinos during the early wet season in the Great Fish River Reserve, South Africa

Plant species	Leaf:stem ratio			
	2 mm	6 mm	10 mm	14 mm
Acacia karroo	0.98[b]	0.53[b]	0.27[b]	0.25[b]
	(0.029)	(0.011)	(0.022)	(0.019)
Azima tetracantha	0.96[b]	0.31[a]	0.19[a]	0.21[b]
	(0.033)	(0.015)	(0.059)	(0.035)
Diospyros lycioides	1.35[c]	0.77[c]	0.44[b]	0.30[b]
	(0.03)	(0.051)	(0.031)	(0.057)
Gymnosporia polyacantha	0.44[a]	0.41[b]	0.37[b]	0.20[b]
	(0.007)	(0.033)	(0.053)	(0.022)
Plumbago auriculata	1.58[c]	0.24[a]	0.20[a]	0.14[a]
	(0.068)	(0.017)	(0.025)	(0.048)

Superscript letters indicate significant differences among plant species according to the least significant difference ($n = 3$; $p < 0.05$).

Table 5
Linear relationships ($y = a + bx$) between twig diameter and dry mass, crude protein and neutral detergent fibre (NDF) of leaves and wood of five woody plants browsed by black rhinos during the early wet season in the Great Fish River Reserve, South Africa ($n = 5$)

y	Plant species	a	b	r^2	p
Dry mass of leaves (g)	*Acacia karroo*	−7.28	2.26	0.73	0.000
	Azima tetracantha	−9.76	2.66	0.70	0.001
	Diospyros lycioides	−2.41	1.58	0.83	0.000
	Gymnosporia polyacantha	−6.21	2.38	0.85	0.000
	Plumbago auriculata	−7.65	2.62	0.81	0.000
Dry mass of wood (g)	*Acacia karroo*	−34.63	9.21	0.77	0.000
	Azima tetracantha	−49.16	12.71	0.78	0.000
	Diospyros lycioides	−16.70	5.38	0.90	0.000
	Gymnosporia polyacantha	−37.70	11.17	0.88	0.000
	Plumbago auriculata	−61.53	17.55	0.88	0.000
Crude protein of leaves (%)	*Acacia karroo*	13.91	−0.10	0.42	0.024
	Azima tetracantha	17.72	−0.22	0.34	0.049
	Diospyros lycioides	13.67	−0.14	0.42	0.023
	Gymnosporia polyacantha	8.71	−0.17	0.51	0.009
	Plumbago auriculata	15.55	0.13	0.17	0.187
Crude protein of wood (%)	*Acacia karroo*	6.51	−0.17	0.66	0.001
	Azima tetracantha	10.96	−0.41	0.86	0.000
	Diospyros lycioides	8.32	−0.33	0.89	0.000
	Gymnosporia polyacantha	6.07	−0.24	0.70	0.001
	Plumbago auriculata	8.38	−0.18	0.39	0.029
NDF of leaves (%)	*Acacia karroo*	42.63	0.50	0.23	0.117
	Azima tetracantha	24.64	0.84	0.16	0.193
	Diospyros lycioides	51.75	0.33	0.15	0.217
	Gymnosporia polyacantha	41.71	−0.18	0.20	0.149
	Plumbago auriculata	54.09	−0.33	0.08	0.384
NDF of wood (%)	*Acacia karroo*	61.85	0.80	0.66	0.001
	Azima tetracantha	47.42	2.03	0.91	0.000
	Diospyros lycioides	54.93	1.15	0.82	0.000
	Gymnosporia polyacantha	57.28	1.64	0.86	0.000
	Plumbago auriculata	62.57	1.13	0.80	0.000

for *D. lycioides*. However, at 14 mm diameter LSR of all species, except *P. auriculata*, was the same.

Linear relationships between twig diameter and leaf DM, wood DM, wood CP and wood NDF were significant for all five species ($p < 0.05$) (Table 5). The relationship between diameter and leaf CP was significant for all species except *P. auriculata* ($p < 0.05$). There were no significant relationships between twig diameter and leaf NDF ($p > 0.05$).

4. Discussion

As found among boreal tree species, CP decreased while fibre increased with increasing twig diameter for the five woody species we studied. The DM of leaves and wood increased

as well. Notably, CP in both leaves and wood of twigs at 6 mm and beyond did not vary much, which coincides with the average diameter of twigs bitten off by the black rhino in thicket vegetation (Ganqa et al., 2005; Wilson and Kerley, 2003). The relatively steep increase in wood fibre with twig diameter was constant, while the DM of leaves and wood increased rapidly above 6 mm diameter. Therefore, in the group of species studied, biting twigs >6 mm in diameter would achieve a greatly increased intake of DM and fibre, offering little benefit in terms of nutrient intake. However, for a large browser such as the black rhino, the possible cost of nutrient intake may be reduced by their ability to efficiently extract energy from low quality forage (Wilson and Kerley, 2003). Furthermore, the rate of increase in fibre and DM, and the concomitant decrease in CP, with twig diameter, tended to be greater for the evergreen species than for the deciduous species. Therefore, the cost of nutrient intake associated with biting large twig sizes is expected to be greater for the evergreen species than for the deciduous species. A black rhino foraging in the GFRR would therefore be expected to select smaller twigs from evergreen species than from deciduous species, with the result that the latter would be subject to greater biomass loss. This needs to be further researched and assessed for consideration in the management of the vegetation and black rhinos.

Generally, CP at all twig diameters varied greatly among the woody species studied. For the larger twig diameters, fibre and LSR varied among species less than for smaller twig diameters, but DM varied more. Like other browsers, which crop smaller bites than what they can potentially crop (Vivås et al. 1991; Wilson and Kerley, 2003), black rhinos typically harvest twigs at the smaller diameters (<6 mm); therefore, fibre concentrations and LSR (leafiness) of their bites vary according to the plant species. CP intake also varies according to species, but the DM of bites varies little among species. Therefore, the black rhino diet selection in GFRR is likely to be affected by a combination of fibre, nutrients and shoot morphology, as suggested elsewhere in the Thicket Biome (Wilson and Kerley, 2003). Because variations among species were most noticeable at smaller twig diameters, and black rhinos are known to take bites smaller than their potential, the ability to select among species is important for them to forage optimally.

According to RD hypotheses, deciduous species are better quality forage for browsers than evergreen species (e.g., Coley and Aide, 1991). However, in our study of five woody species, this was not apparent. Of the two evergreen species included in the study, one had low CP, but the other had high CP relative to the remaining species studied. Of the three deciduous species, one had high CP (*P. auriculata*), but the others (*Acacia karroo* and *D. lycioides*) were intermediate in the observed range of values. In contrast, leaf fibre tended to vary according to canopy retention pattern, but not in a way that would be expected. The deciduous species consistently had higher leaf fibre than the evergreen species had. Wood fibre did not follow the same pattern. Our observations of the above trends support those of other studies that have found that canopy retention pattern among woody species in semi-arid subtropical systems is not consistently related to forage quality, probably because of the high spatial and temporal heterogeneity of semi-arid systems (Nelson et al., 2002; Scogings et al., 2004).

Alternatively, quality among the species studied could be related to potential bud activity, which is related to resource availability (Herms and Mattson, 1992) and ultimately determines plant architecture (Bell et al., 1999). Active meristematic tissues require large quantities of nutrients and water to drive cell division and growth, and growing shoots therefore constitute strong resource sinks (Herms and Mattson, 1992). Therefore,

species that depend on active apical buds to extend internodes and thus add new leaf area (LS species) should have higher concentrations of nutrients than species that simply add new leaf area without shoot elongation (SS species). Except for *D. lycioides*, the LS species did tend to have higher CP than the SS species had within the group of studied species.

Because of their potential nutrient richness, long shoots are both valuable to plants and vulnerable to herbivores (Rhoades, 1979). It follows, therefore, that the LS species require mechanisms of avoiding herbivory (Rhoades, 1979). One mechanism of defence is fibre, which enhances toughness and reduces browsing (Jung and Allen, 1995; Shipley and Spalinger, 1992). Except for *Azima tetracantha*, leaf fibre did tend to be higher for the LS species, than for the SS species. However, black rhinos have been observed to prefer species high in fibre (Muya and Oguge, 2000). Therefore, the effectiveness of fibre as a defence against browsers in the particular group of species studied depends on the species of the browser. The measured forage quality characteristics were not consistently related to either canopy retention patterns or shoot growth patterns found among the species studied. More samples from a larger group of subtropical species, and with a broader suite of chemical characteristics determined (e.g., tannins, phenols, cellulose and lignin), would clarify relationships among forage characteristics and growth habits, leading to better understanding of browse–browser interactions in semi-arid subtropical systems.

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