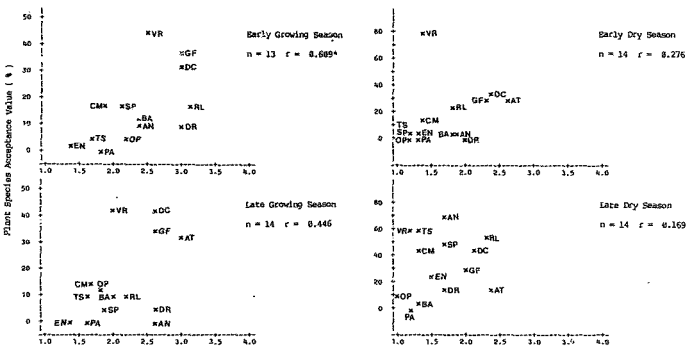


Fig 7.1. The Acceptance of Woody Plant Species in Relation to the Concentration of Nitrogen in the Leaves.

1. Kudus

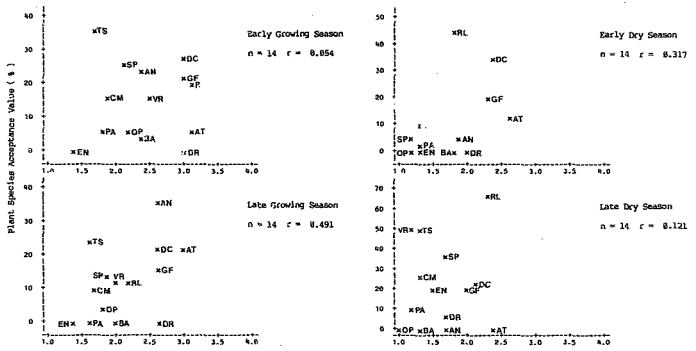


Fig 7.1. The Acceptance of Woody Plant Species in Relation to the Concentration of Nitrogen in the Leaves.

ii. Impalas

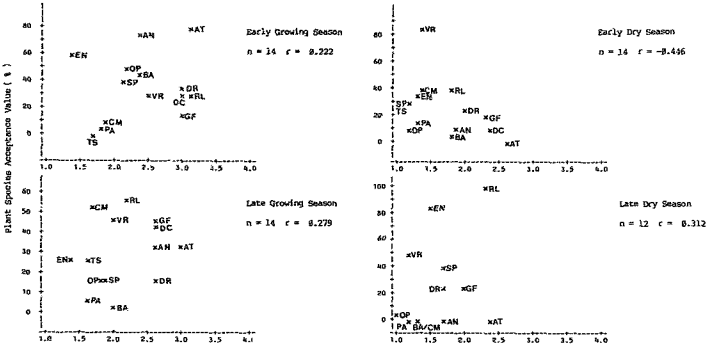


Fig 7.1. The Acceptance of Woody Plant Species in Relation to the Concentration of Nitrogen in the Leaves.

iii. Goats

Table 7.1. Differences Between the Nitrogen Concentration (% Dry Weight) in the Leaves of Favoured and Non-preferred Woody Plant Species

i. Kudus

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	2.7	± 0.4	2.1	± 0.5	11	1.704
Late Growing Season	2.6	± 0.4	1.9	± 0.4	12	3.627*
Early Dry Season	2.1	± 0.5	1.5	± 0.3	12	2.915*
Late Dry Season	1.6	± 0.4	1.6	± 0.5	12	0.213

ii. Impalas

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	2.6	± 0.5	2.3	± 0.6	12	0.894
Late Growing Season	2.4	± 0.6	1.9	± 0.4	12	2.019*
Early Dry Season	1.9	± 0.5	1.5	± 0.5	12	0.847
Late Dry Season	1.6	± 0.5	1.9	± 0.5	12	0.059

iii. Goats

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	2.3	± 0.6	2.4	± 0.6	12	0.450
Late Growing Season	2.4	± 0.5	1.8	± 0.4	12	2.373*
Early Dry Season	1.4	± 0.2	1.9	± 0.5	12	1.697
Late Dry Season	1.7	± 0.5	1.5	± 0.4	11	0.471

* Significant at 95% by the Randomisation Test

Table 7.1.b. Woody Plant Species Favoured by the Animals in each Season.

Season	Kudus	Impalas	Goats
Early Growing		Acacia nilotica	Acacia nilotica
Season	Grewia flavescens	Grewia flavescens	Acacia tortilis
	Dichrostachys cinerea	Dichrostachys cinerea	Burkea africana
	Vitex rehmannii	Terminalia sericea	Euclea natalensis
	Rhus leptodictya	Rhus leptodictya	Ochna pulchra
	Strychnos pungens	Strychnos pungens	
Late Growing	Acacia nilotica	Acacia nilotica	Acacia nilotica
Season	Acacia tortilis	Acacia *tortilis*	*Acacia tortilis*
	Dichrostachys cinerea	Dichrostachys cinerea	Dichrostachys cinerea
	Grewia flavescens	Grewia flavescens	*Grewia flavescens*
	Vitex rehmannii	Terminalia sericea	Vitex rehmannii
			Rhus leptodictya
			Combretum molle
Early Dry	Acacia tortilis	Combretum molle	Combretum molle
Season	Dichrostachys cinerea	Dichrostachys cinerea	Euclea natalensis
	Grewia flavescens	Grewia flavescens	Terminalia sericea
	Rhus leptodictya	Rhus leptodictya	Rhus leptodictya
	Vitex rehmannii	Vitex rehmannii	Vitex rehmannii
Late Dry	Rhus leptodictya	Rhus leptodictya	Rhus leptodictya
Season	Strychnos pungens	Strychnos pungens	Strychnos pungens
	Terminalia sericea	Terminalia sericea	Euclea natalensis
	Vitex rehmannii	Vitex rehmannii	Vitex rehmannii
	Acacia nilotica		
	Combretum molle		

correlated to the nitrogen concentration (Fig 7.1.ii.), although in the late growing season the favoured species were of higher protein content than the group of less preferred plants (Table 7.1.). In the dry season several protein poor species were of high acceptance to the impalas.

iii. Goats

The nitrogen rich Acacia species were of high acceptance to the goats in the early growing season along with several species of low nitrogen content (Fig 7.1.iii.). Although nitrogen concentration was not significantly correlated to acceptance in any season, the species favoured by the goats in the late growing season were on average, richer in nitrogen than those species of low acceptance (Table 7.1.). No pattern existed between acceptance and nitrogen contents in the dry season.

iv. Plant Species Differences

Of the species high in nitrogen D. rotundifolia was unusual in being of consistently low acceptance to all the animals. Most of the nitrogen rich plants were favoured in the growing season, although the thorny Acacias were of rather lower acceptance, especially to the kudus, than were non-thorny plants of similar nitrogen content.

V. rehmannii was favoured, particularly in the dry seasons, yet was of moderate to low nitrogen content. O. pulchra and P.

africanum contained very low nitrogen concentrations and was of low acceptance. Other nitrogen poor species were eaten increasingly as the dry season progressed and food availability declined. O. pulchra and B. africana were eaten only as new leaves when they were comparatively rich in nitrogen. On maturit the nitrogen content and acceptance decreased.

b. Phosphorus

i. Kudus

The phosphorus content of the foliage of woody plants was not significantly correlated to acceptance by the kudus, except in the early growing season when a positive relationship existed (Fig 7.2.i.). If D. rotundifolia was excluded from the correlation the relationship became much stronger ($r = 0.880^{***}$). The favoured species in the early dry season were on average richer in phosphorus than non-preferred species, but no pattern was evident in the other seasons (Table 7.1.).

ii. Impalas

The acceptance of plants by impalas was only significantly correlated to the phosphorus content in the early dry season (Fig 7.2.ii.). This was due to a high acceptance for the phosphorus rich plant R. leptodictya. The average phosphorus concentration of preferred plants was not significantly different to that of less favoured species (Table 7.2.).

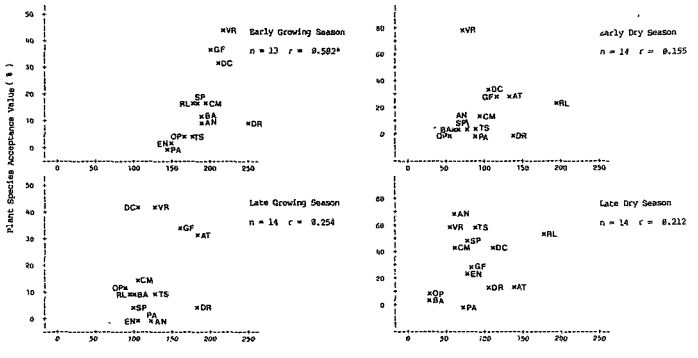


Fig 7.2. The Acceptance of Woody Plant Species in Relation to the Concentration of Phosphorus in the Leaves.

1. Kudus

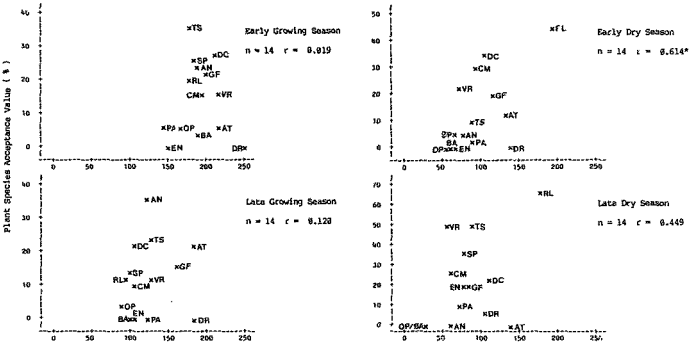


Fig 7.2. The Acceptance of Woody Plant Species in Relation to the Concentration of Phosphorus in the Leaves.

ii. Impalas

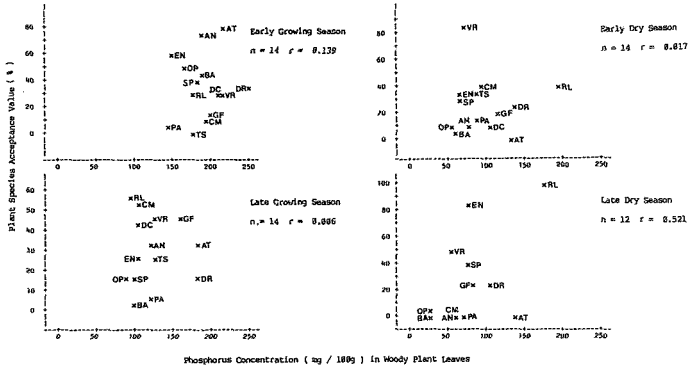


Fig 7.2. The Acceptance of Woody Plant Species in Relation to the Concentration of Phosphorus in the Leaves.

iii. Goats

Table 7.2. Differences Between the Phosphorus Concentration (mg / 100g) in the Leaves of Favoured and Non-preferred Woody Plant Species

i. Kudus

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	198.0	± 17.2	182.6	± 32.1	11	0.994
Late Growing Season	140.2	± 32.0	115.6	± 29.1	12	1.468
Early Dry Season	125.0	± 44.6	81.9	± 25.9	12	2.321*
Late Dry Season	88.0	± 45.4	80.8	± 38.2	12	0.410

ii. Impalas

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	190.2	± 14.5	190.9	± 35.5	12	0.045
Late Growing Season	139.8	± 32.2	115.8	± 29.2	12	1.432
Early Dry Season	117.2	± 46.3	86.2	± 31.0	12	1.514
Late Dry Season	110.3	± 53.2	76.9	± 34.7	12	1.035

iii. Goats

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	183.8	± 24.4	194.8	± 29.7	12	0.755
Late Growing Season	128.7	± 32.9	120.1	± 31.7	12	0.494
Early Dry Season	103.8	± 52.4	93.7	± 31.7	12	0.456
Late Dry Season	97.8	± 53.7	72.6	± 36.9	10	1.005

* Significant at 95% by the Randomisation Test

iii. Goats

At no time was the acceptance of woody plants by goats correlated to the phosphorus content of the foliage (Fig 7.2.iii.), nor were the favoured plants of higher phosphorus content than non-preferred species (Table 7.2.).

vi. Plant Species Differences

Plants rich in phosphorus were not especially favoured by the animals. Both A. tortilis and the non-preferred plant D. rotundifolia were very rich in this mineral. Leaves of D. cinerea and V. rehmannii were rich in phosphorus only in the immature phase but were favoured throughout the year. Unlike most other woody species R. leptodictya showed little seasonal decline in phosphorus content, hence was of relatively high phosphorus content in the dry season when it was favoured by the animals.

c. Potassium

i. Kudus

The potassium concentration of woody plant leaves was not significantly correlated to their acceptance by kudus (Fig 7.3.i.). In the late growing season those plants very low in potassium were not favoured. The difference between the acceptance of high and low potassium species only became significant in the early dry season, and disappeared again in the late dry season with the increased use of less nutrient rich species (Table 7.3.).

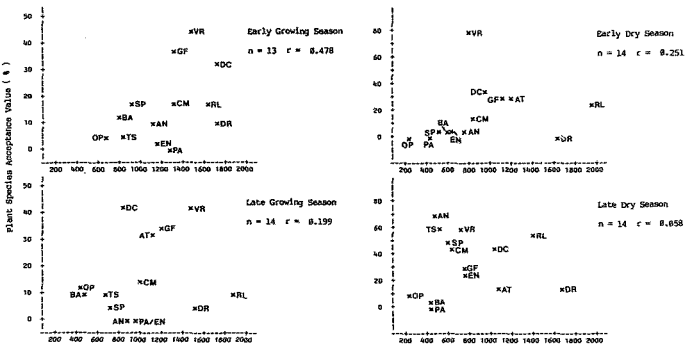


Fig 7.3. The Acceptance of Woody Plant Species in Relation to the Concentration of Potassium in the Leaves.

1. Kudus

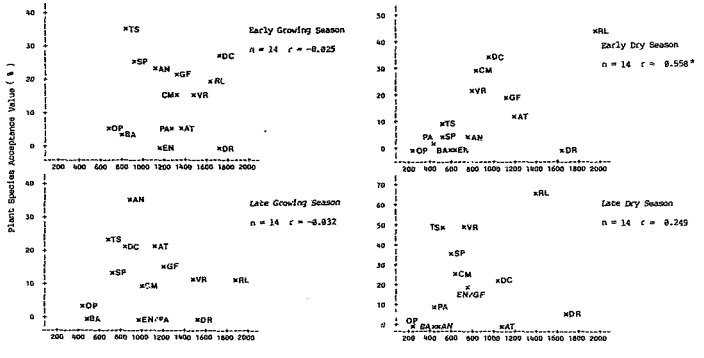


Fig 7.3. The Acceptance of Woody Plant Species in Relation to the Concentration of Potassium in the Leaves.

ii. Impalas

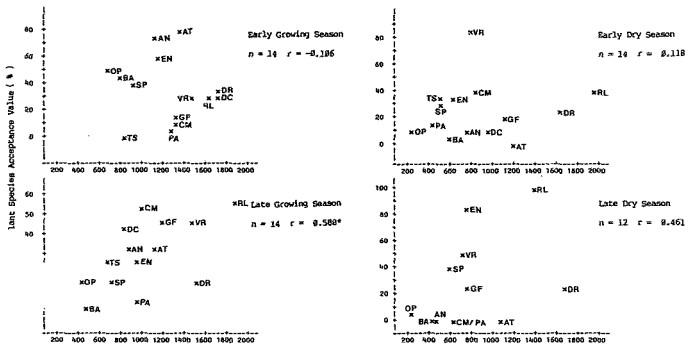


Fig 7.3. The Acceptance of Woody Plant Species in Relation to the Concentration of Potassium in the Leaves.

iii. Goats

Table 7.3. Differences Between the Potassium Concentration (mg / 100g) in the Leaves of Favoured and Non-preferred Woody Plant Species

i. Kudus

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	1408.4	± 315.9	1112.9	± 339.9	11	1.552
Late Growing Season	1108.8	± 266.1	958.4	± 467.1	12	0.657
Early Dry Season	1207.8	± 445.1	685.2	± 404.4	12	2.253*
Late Dry Season	721.8	± 344.4	880.8	± 464.9	12	0.350

ii. Impalas

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	1256.5	± 360.0	1220.8	± 346.8	12	0.188
Late Growing Season	949.4	± 216.2	1047.0	± 485.2	12	0.422
Early Dry Season	1135.8	± 473.5	725.7	± 439.2	12	1.630
Late Dry Season	809.3	± 404.3	750.0	± 425.2	12	0.239

iii. Goats

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	1128.2	± 351.5	1323.0	± 324.0	12	1.122
Late Growing Season	1201.7	± 364.9	882.6	± 365.0	12	1.612
Early Dry Season	950.6	± 578.3	828.1	± 446.2	12	0.445
Late Dry Season	867.0	± 367.6	710.4	± 466.9	10	0.578

* Significant at 95% by the Randomisation Test

ii. Impalas

The acceptance of plant species by impalas was positively correlated to the potassium content in the early dry season only. This was mainly due to the high acceptance of R. leptodictya (Fig 7.3.ii.). Several other species with high potassium contents were of low acceptance. The preferred species were not significantly richer in potassium than less favoured species (Table 7.3.).

iii. Goats

The potassium concentration in woody plant leaves only correlated with their acceptance to goats in the late growing season (Fig 7.3.iii.). In this season most of the favoured plants were rich in potassium but on average were not quite significantly different to the less preferred species (Table 7.3.).

iv. Plant Species Differences

D. rotundifolia and R. leptodictya both contained high concentrations of potassium, but D. rotundifolia was consistently non-preferred and R. leptodictya was only of high acceptance in the dry season. V. rehmannii and [illegible] remained of high acceptance throughout the year, despite a rapid decrease in the potassium content of the leaves upon attaining full size. Species of very low potassium content were generally of low acceptance, these include B. africana, O. pulchra and P. africanum.

d. Calcium

i. Kudus

The acceptance of woody plants by kudus was not significantly correlated to the calcium content of the leaves (Fig 7.4.i.). In all but the late dry season several of the favoured species tended to be fairly rich in calcium, but this pattern was only significant in the late growing season (Table 7.4.). Species very poor in calcium were of consistently low acceptance to the kudus.

ii. Impalas

The impalas, like the kudus, showed no significant correlation between the acceptance of plant species and the calcium concentrations in the leaves (Fig 7.4.ii.). In the late growing and early dry period several favoured plants were of moderate to high calcium content,but the difference between the favoured and non-preferred groups of plants was not significant (Table 7.4.).

iii. Goats

The goats showed a similar pattern to the kudus. No significant correlations were found between the calcium content of woody plants and their acceptance to goats (Fig 7.4.iii.). In all but the late dry season, when previously non-preferred plants increased in acceptance, the favoured plants tended to be fairly

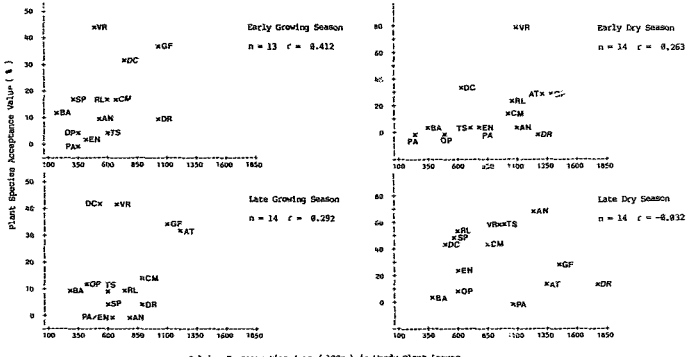


Fig 7.4. The Acceptance of Woody Plant Species in Relation to the Concentration of Calcium in the Leaves.

1. Kudus

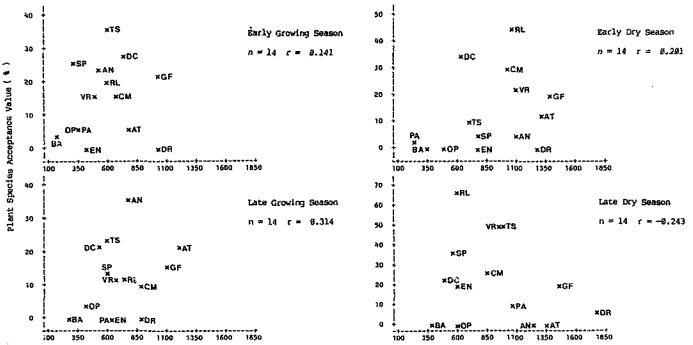


Fig 7.4. The Acceptance of Woody Plant Species in Relation to the Concentration of Calcium in the Leaves.

ii. Impalas

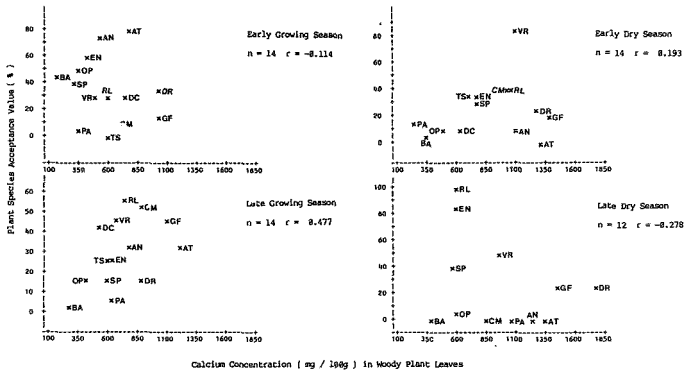


Fig 7.4. The Acceptance of Woody Plant Species in Relation to the Concentration of Calcium in the Leaves.

iii. Goats

Table 7.4. Differences Between the Calcium Concentration (mg / 100g) in the Leaves of Favoured and Non-preferred Woody Plant Species

i. Kudus

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	519.5	± 269.2	539.6	± 263.1	11	0.366
Late Growing Season	856.4	± 299.6	631.2	± 195.8	12	1.806*
Early Dry Season	1104.4	± 292.3	860.9	± 325.8	12	1.388
Late Dry Season	865.3	± 251.9	967.0	± 519.4	12	0.441

ii. Impalas

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	597.3	± 243.2	560.7	± 280.0	12	0.251
Late Growing Season	841.4	± 312.8	639.6	± 195.7	12	1.503
Early Dry Season	1044.2	± 265.5	894.3	± 358.3	12	0.815
Late Dry Season	775.3	± 220.5	982.7	± 468.2	12	0.766

iii. Goats

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	454.8	± 224.8	648.0	± 251.9	12	1.427
Late Growing Season	846.0	± 248.0	577.3	± 185.7	12	2.278*
Early Dry Season	935.8	± 177.5	954.6	± 396.0	12	0.100
Late Dry Season	681.0	± 174.4	1089.4	± 464.5	10	1.656

* Significant at 95% by the Randomisation Test

rich in calcium, but only in the late growing season did the difference in the average calcium content of preferred and non-preferred plants become significant (Table 7.4.).

iv. Plant Species Differences

Many of the plants favoured by the animals were comparativly rich in calcium yet D. rotundifolia was not favoured despite the high concentration of calcium in the leaves. Conversely the generally favoured plant D. cinerea was not rich in calcium once the leaves had matured. V. rehmannii was also of high acceptance to the kudus and goats, both in the growing season when it was fairly low in calcium and in the dry season when the calcium [illegible] as much higher.

e. Magnesium

i. Kudus

The woody plant species of high acceptance to the kudus were often those rich in magnesium. The correlation between plant species acceptance by kudus and the magnesium concentration in the leaves was significantly positive in the early growing and early dry seasons (Fig 7.5.i.). The pattern was broken in the late growing season by the low acceptance of several magnesium rich species, while in the late dry season, some low magnesium species were highly favoured.

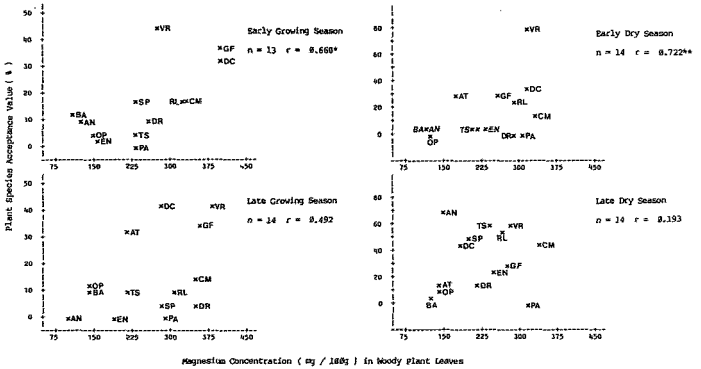


Fig 7.5. The Acceptance of Woody Plant Species in Relation to the Concentration of Magnesium in the Leaves.

1. Kudus

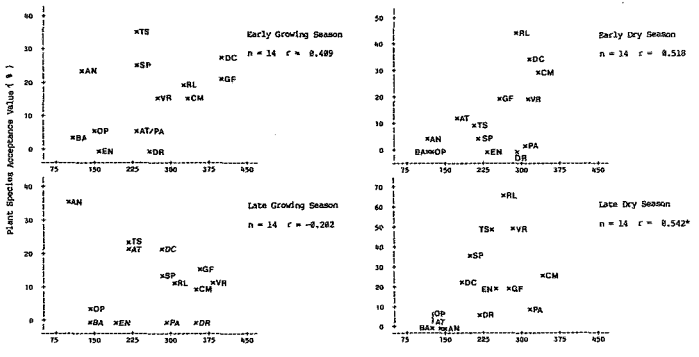


Fig 7.5. The Acceptance of Woody Plant Species in Relation to the Concentration of Magnesium in the Leaves.

ii. Impalas

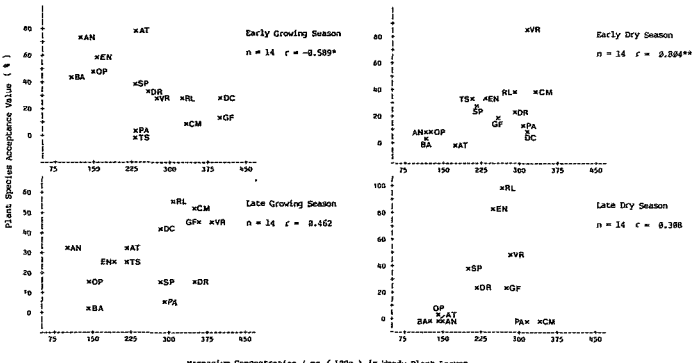


Fig 7.5. The Acceptance of Woody Plant Species in Relation to the Concentration of Magnesium in the Leaves.

iii. Goats

Table 7.5. Differences Between the Magnesium Concentration (mg / 100g) in the Leaves of Favoured and Non-preferred Woody Plant Species

i. Kudus

	Favoured		*Non-Preferred*			
	Mean	SE	Mean	SE	df	t
Early Growing Season	327.0 ±	73.6	199.9 ±	77.8	11	2.956*
Late Growing Season	267.8 ±	114.3	252.4 ±	81.6	12	0.295
Early Dry Season	312.6 ±	126.0	216.2 ±	83.5	12	1.737*
Late Dry Season	247.5 ±	67.4	206.4 ±	69.0	12	1.117

ii. Impalas

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	285.8 ±	108.8	218.8 ±	75.0	12	1.372
Late Growing Season	234.4 ±	95.0	271.0 ±	90.7	12	0.713
Early Dry Season	344.4 ±	99.5	198.6 ±	71.7	12	3.192*
Late Dry Season	294.0 ±	36.8	214.0 ±	77.7	12	0.848

iii. Goats

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	154.2 ±	47.7	299.3 ±	68.3	12	4.451*
Late Growing Season	285.3 ±	98.7	230.6 ±	78.9	12	1.137
Early Dry Season	316.4 ±	122.0	214.1 ±	83.7	12	1.873*
Late Dry Season	250.8 ±	36.4	213.4 ±	86.5	10	0.808

* Significant at 95% by the Randomisation Test

ii. Impalas

For the impalas the correlation between plant species acceptance and magnesium content only approached significance in the dry season (Fig 7.5.ii.). Although the favoured group of plants were on average significantly richer in magnesium than non-preferred species only in the early dry season (Table 7.5.), the regression failed to reach significance due to the low acceptance of V. rehmannii. By the late dry season, however, a significant positive correlation had developed.

iii. Goats

A weakly significant negative correlation existed between the acceptance of woody plants by goats and the magnesium content in the early growing season (Fig 7.5.iii.). This was due to their high acceptance of E. natalensis and the magnesium poor Acacia species. By the late growing season, this pattern was reversing and a strongly positive correlation had developed by the early dry season. Much of this correlation was due to the extreme value of V. rehmannii. The correlation no longer existed in the late dry season when the two most highly accepted plants were only of moderate magnesium content.

iv. Plant Species Differences

Most of the woody plants favoured by the animals had a high magnesium content. The non-preferred plant D. rotundifolia was

also comparatively rich in magnesium, as in all other minerals. P. africanum was of fairly high magnesium content in the late dry season, but was of low acceptance. A. nilotica was favoured despite the low magnesium content. This species is rich in most other minerals.

f. Sodium

i. Kudus

The acceptance of woody plants by kudus was not significantly correlated to the sodium content (Fig 7.6.i.). In the early dry season the preferred species were significantly richer in sodium than less preferred plants (Table 7.6.).

ii. Impalas

No correlation was found between plant species acceptance and sodium content (Fig 7.6.ii.), but in the late growing season, the impalas tended to favour several of the species richest in sodium. However, the difference in the average sodium content of preferred and non-preferred plants was not significant (Table 7.6.).

iii. Goats

The goats favoured the sodium rich A. nilotica species in the early growing season, but otherwise the sodium content of the plants did not appear to be related to acceptance (Fig 7.6.iii.). In the late

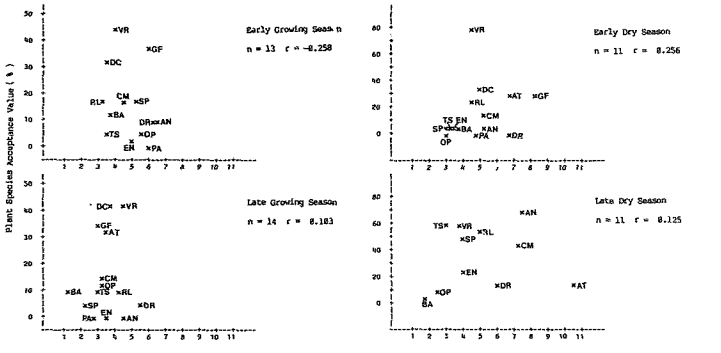


Fig 7.6. The Acceptance of Woody Plant Species in Relation to the Concentration of Sodium in the Leaves.

i. Kudus

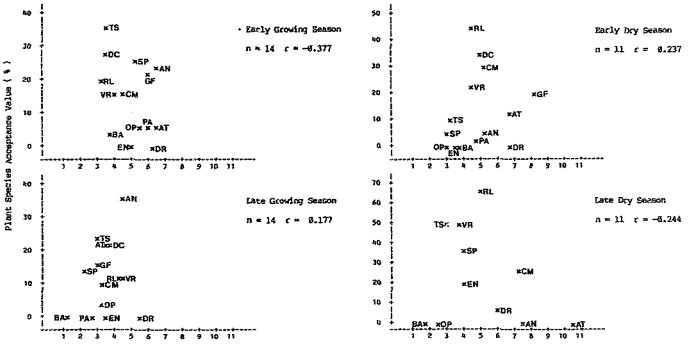


Fig 7.6. The Acceptance of Woody Plant Species in Relation to the Concentration of Sodium in the Leaves.

ii. Impalas

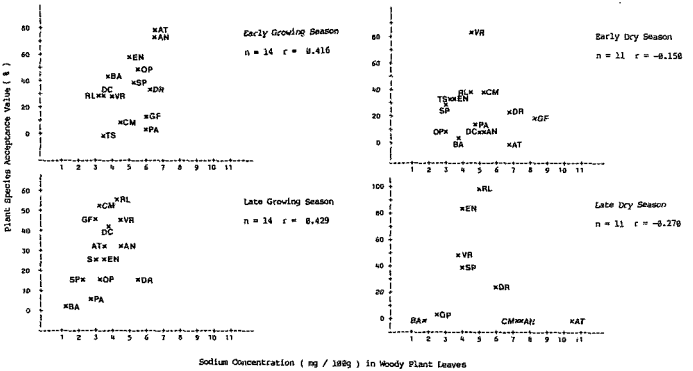


Fig 7.6. The Acceptance of Woody Plant Species in Relation to the Concentration of Sodium in the Leaves.

iii. Goats

Table 7.6. Differences Between the Sodium Concentration (mg / 100g) in the Leaves of Favoured and Non-preferred Woody Plant Species

i. Kudus

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	4.4 ±	1.2	5.2 ±	1.2	11	1.168
Late Growing Season	3.9 ±	1.6	3.2 ±	1.2	12	1.218
Early Dry Season	5.8 ±	1.7	4.3 ±	1.3	12	1.891*
Late Dry Season	5.1 ±	1.9	4.9 ±	3.5	9	0.112

ii. Impalas

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	4.7 ±	1.5	5.2 ±	1.1	12	0.756
Late Growing Season	3.6 ±	0.7	3.4 ±	1.3	12	0.328
Early Dry Season	5.5 ±	1.6	4.4 ±	1.5	12	1.283
Late Dry Season	3.9 ±	0.8	5.6 ±	3.1	9	1.048

iii. Goats

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	5.5 ±	1.2	4.7 ±	1.2	12	1.186
Late Growing Season	3.8 ±	0.6	3.1 ±	1.3	12	1.276
Early Dry Season	4.2 ±	0.8	5.3 ±	1.8	12	1.156
Late Dry Season	4.2 ±	0.6	5.9 ±	3.3	8	0.985

* Significant at 95% by the Randomisation Test

dry season the species of highest acceptance contained little sodium.

iv. Plant Species Differences

The most sodium rich plants were G. flavescens, D. rotundifolia and the Acacia species. Of these only D. rotundifolia was of consistently low acceptance. D. cinerea and V. rehmannii were not rich in sodium yet were favoured plant species.

g. Moisture

i. Kudus

There was no significant correlation between the water content of plant species and their acceptance to kudus (Fig 7.7.i.). In the late dry and early growing seasons some of the favoured plants had fairly high water contents but on average there was no significant difference between the preferred and non-preferred groups of plants (Table 7.7.).

ii. Impalas

Impalas, like the kudus, showed no correlation between the acceptance of plant species and the moisture content (Fig 7.7.ii.). However in the dry season some of the favoured species were of high moisture content although this difference was not significant (Table 7.7.).

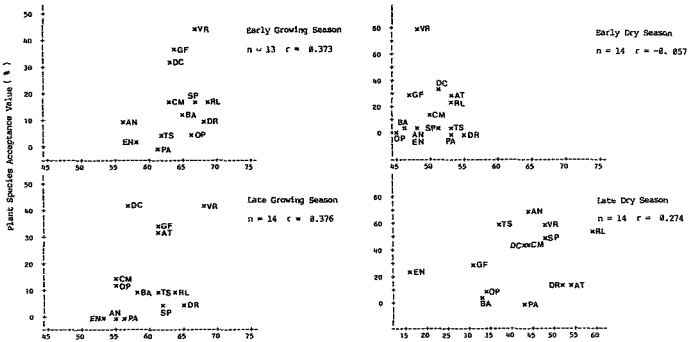


Fig 7.7. The Acceptance of Woody Plant Species in Relation to the Concentration of Moisture in the Leaves.

1. Kudus

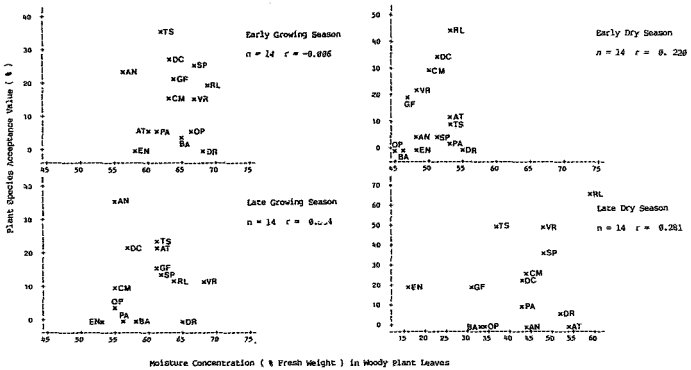


Fig 7.7. The Acceptance of Woody Plant Species in Relation to the Concentration of Moisture in the Leaves.

ii. Impalas

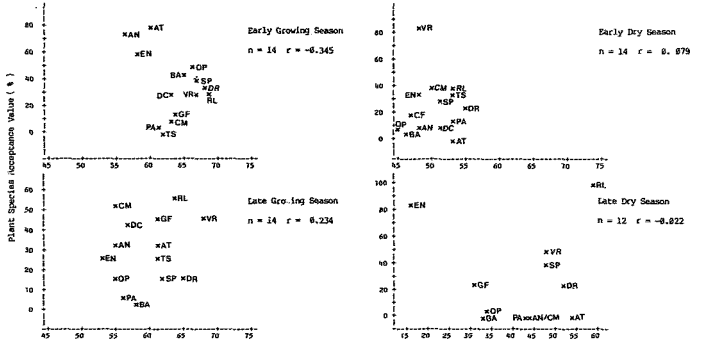


Fig 7.7. The Acceptance of Woody Plant Species in Relation to the Concentration of Moisture in the Leaves.

iii. Goats

Table 7.7. Differences Between the Moisture Concentration (% Fresh Weight) in the Leaves of Favoured and Non-preferred Woody Plant Species

i. Kudus

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	66.0	± 2.4	62.4	± 4.0	11	1.634
Late Growing Season	60.4	± 5.0	58.8	± 4.4	12	0.600
Early Dry Season	50.4	± 2.8	49.6	± 4.0	12	0.392
Late Dry Season	46.7	± 7.3	38.3	± 12.4	12	1.477

ii. Impalas

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	63.5	± 4.5	63.5	± 3.5	12	0.000
Late Growing Season	59.0	± 2.8	59.6	± 5.3	12	0.232
Early Dry Season	49.8	± 2.4	49.9	± 4.2	12	0.049
Late Dry Season	48.0	± 9.0	39.4	± 11.2	12	1.332

iii. Goats

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	61.0	± 4.4	64.9	± 2.9	12	2.030*
Late Growing Season	60.1	± 4.8	58.6	± 4.3	12	0.488
Early Dry Season	48.0	± 1.2	49.6	± 4.1	12	0.786
Late Dry Season	42.8	± 18.6	41.9	± 8.6	10	0.117

* Significant at 95% by the Randomisation Test

iii. Goats

For the goats, plant species acceptance showed no correlation with moisture content (Fig 7.7.iii.). The preferred species in the early growing season in fact had a significantly lower moisture content than the less preferred species (Table 7.7.).

vi. Plant Species Differences

The driest leaves belonged to those plants with finely divided leaves, namely A. nilotica, A. tortilis, D. cinerea and P. africanum, which show a variety of acceptance values. D. rotundifolia and R. leptodictya leaves contained most moisture in the dry season, but only R. leptodictya was of high acceptance.

h. Summary: The Acceptance of Woody Plant Species in Relation to Nutrient Concentrations

i. The acceptance of woody plant species by browsing ungulates was rarely significantly correlated to the nutrient concentrations in the plants, although the preferred plants were often comparatively rich in nutrients.

ii. Plant species acceptance was most clearly related to nitrogen and magnesium contents.

iii. The kudus showed a weak, but significant positive correlation

between the acceptance of woody plants in the early growing season and the nitrogen, phosphorus, and magnesium contents. The impalas and goats showed no relationship between nutrient concentration and acceptance in this season.

iv. The acceptance of plant species was not significantly correlated to nutrient contents in the late growing season. However, the favoured plants were of significantly higher average nitrogen content than the non-preferred species. The kudus and goats also favoured plants of above average calcium content.

v. In the early dry season the kudus alone showed a significant preference for nitrogen rich plants. There was a significant correlation between the magnesium content of woody plants and the acceptance by kudus and goats, due mainly to their high acceptance of V. rehmannii. The impalas showed a significant correlation between acceptance and the phosphorus and potassium contents of the plants, but again, this was due mainly to a high acceptance of one species, R. leptodictya. The kudus also favoured those plants rich in phosphorus and potassium.

vi. In the late dry season when food availability was low, the acceptance of the animals for less nutrient rich plant species increased. The only significant relationship between acceptance and nutrient concentrations was a positive correlation between magnesium concentration and acceptance by

impala.

vii. Most plants with above average nutrient contents were in the more preferred group of woody plants. The exception was D. rotundifolia, which is rich in all nutrients assayed, yet remained of low acceptance. Generally D. cinerea and V. rehmannii were favoured food plants, yet were of above average concentration in only two nutrients namely nitrogen and magnesium for D. cinerea and calcium and magnesium for V. rehmannii. Plant species of consistently low mineral content were not favoured.

B. Forbs

a. Nitrogen

i. Kudus

There was no correlation between the acceptance of common forbs by kudus and the nitrogen content of the whole plants (Fig 7.8.i.), nor did the favoured species contain greater concentrations of nitrogen than non-preferred species (Table 7.8.).

ii. Impalas

The acceptance of forbs by impalas was not significantly correlated to the nitrogen content (Fig 7.8.ii.). In the dry season the favoured plants were of comparatively low nitrogen

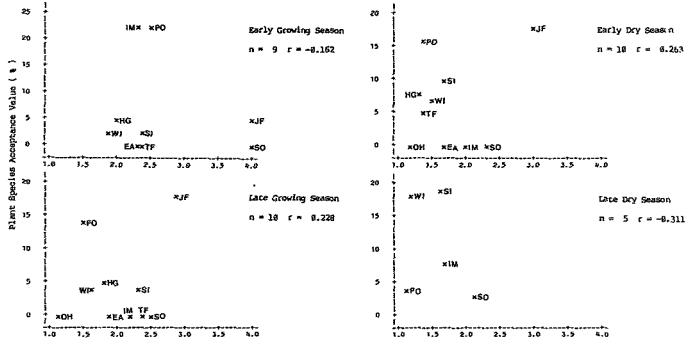


Fig 7.8. The Acceptance of Forb Species in Relation to the Concentration of Nitrogen in Whole Plants.

1. Rudus

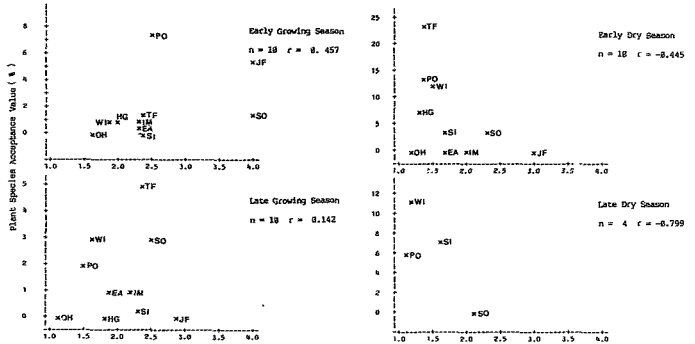


Fig 7.8. The Acceptance of Forb Species in Relation to the Concentration of Nitrogen in Whole Plants.

ii. Impalas

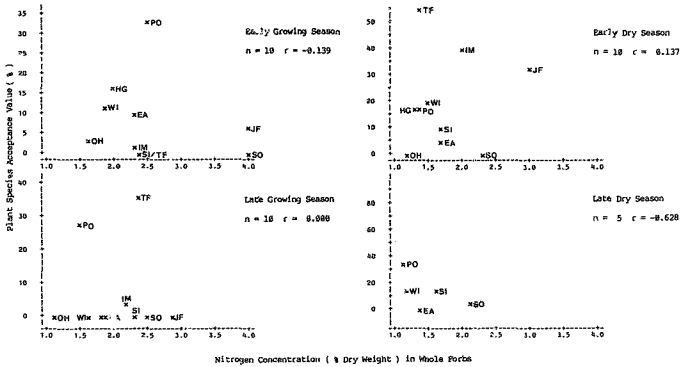


Fig 7.8. The Acceptance of Forb Species in Relation to the Concentration of Nitrogen in Whole Plants.

iii. Goats

Table 7.8. Differences Between the Nitrogen Concentration (% Dry Weight) in Favoured and Non-preferred Forb Species

i. Kudus

	Favoured		Non-Preferred			
	Mean	*SE*	*Mean*	*SE*	*df*	*t*
Early Growing Season	2.4 ±	0.2	2.7 ±	0.9	7	0.458
Late Growing Season	2.2 ±	1.0	2.0 ±	0.5	8	0.432
Early Dry Season	1.6 ±	0.8	1.6 ±	0.4	8	1.134
Late Dry Season	1.4 ±	0.2	1.6 ±	0.5	3	0.657

ii. Impalas

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	3.3 ±	1.0	2.3 ±	0.7	8	1.496
Late Growing Season	2.0 ±	0.5	2.0 ±	0.6	8	0.175
Early Dry Season	1.4 ±	0.4	1.9 ±	0.6	8	1.177
Late Dry Season	1.3 ±	0.2	1.8 ±	0.5	3	1.541

iii. Goats

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	2.3 ±	0.7	2.7 ±	1.0	8	0.663
Late Growing Season	1.9 ±	0.6	2.0 ±	0.5	8	0.285
Early Dry Season	2.1 ±	0.8	1.5 ±	0.4	8	1.621
Dry Season	1.1 ±	-	1.6 ±	0.4	3	1.329

* significant at 95% by the Randomisation Test

Table 7.5.b. *Forb Species Favoured* by the Animals in each Season.

Season	Kudus	Impalas	Goats
Early Growing Season	Pollichia campestris	Pollichia campestris	Pollichia campestris
	Indigofera macra	Justicia flava	Hermannia grisea
			Evolvulus alsinoides
			Waltheria indica
Late Growing Season	Pollichia campestris	Pollichia campestris	Pollichia campestris
	Justicia flava	Tephrosia forbesii	Tephrosia forbesii
		Solanum panduraeforme	
		Waltheria indica	
Early Dry Season	*Pollichia campestris*	*Pollichia campestris*	*Pollichia campestris*
	Justicia flava	Tephrosia forbesii	Tephrosia forbesii
	Sida cordifolia	Waltheria indica	Justicia flava
Late Dry Season	Sida cordifolia	Sida cordifolia	Justicia flava
	Hermannia grisea	Pollichia campestris	Pollichia campestris
	Waltheria indica	Waltheria indica	Hermannia grisea

content.

iii. Goats

For the goats there was no significant correlation between acceptance and the nitrogen concentration of forbs (Fig 7.8.iii.). In the dry season the favoured plants were of rather low nitrogen content.

iv. Plant Species Differences

P. campestris was generally of high acceptance to the animals but was not particularly rich in nitrogen. The nitrogen content of T. forbesii was initially high in the late growing season, but rapidly decreased, yet the impalas and goats continued to favour this species regardless of the change in nitrogen content. T. forbesii was uncommon in the year that the kudus were studied. The most nitrogen rich plants were J. flava and S. pandureaforme. S. pandureaforme was of consistently low acceptance, while J. flava was favoured by the impalas only in the early growing season and by the kudus in the late growing and early dry seasons. J. flava was not often encountered by the goats in the growing season, but was eaten as bare stalks in the late dry season. O. herbacea was of very low nitrogen concentration relative to other forbs and was rarely eaten.

b. Phosphorus

i. Kudus

The phosphorus concentration in forbs was not correlated to their acceptance by kudus (Fig 7.9.i.). Plants of both low and high phosphorus content were favoured.

ii. Impalas

The acceptance of forbs by impalas was not significantly correlated to the phosphorus content of the plants (Fig 7.9.ii). Favoured species contained a wide range of phosphorus concentrations.

iii. Goats

As for the other animals the acceptance of forbs by goats was not correlated to the phosphorus content (Fig 7.9.iii.). In the dry season low phosphorous content plants were often favoured over species richer in this mineral.

iv. Plant Species Differences

P. campestris was of high acceptance to all the animals throughout the growing and early dry seasons, yet was only of high phosphorus content in the preflowering phase. Thereafter it was of relatively low phosphorus content. The impalas and goats also favoured T.

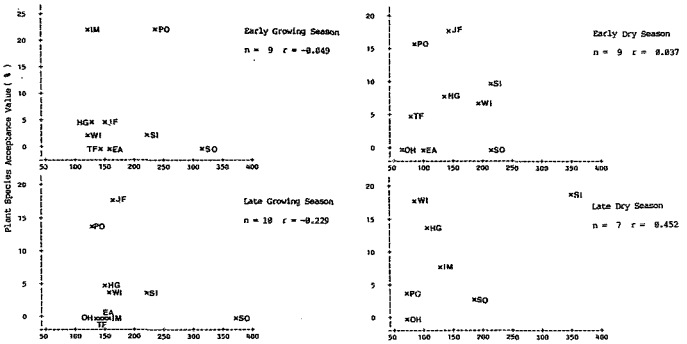


Fig 7.9. The Acceptance of Forb Species in Relation to the Concentration of Phosphorus in Whole Plants.

i. Eadus

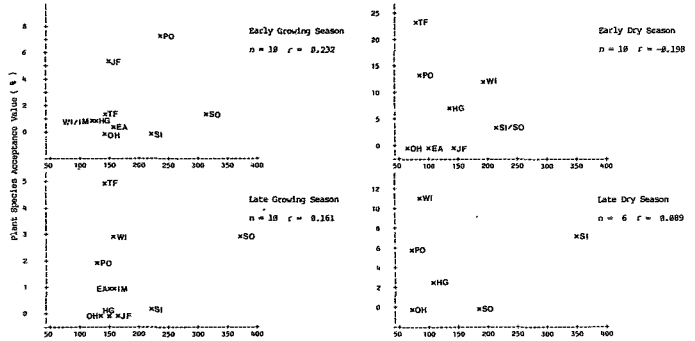


Fig 7.9. The Acceptance of Forb Species in Relation to the Concentration of Phosphorus in Whole Plants.

ii. Impalas

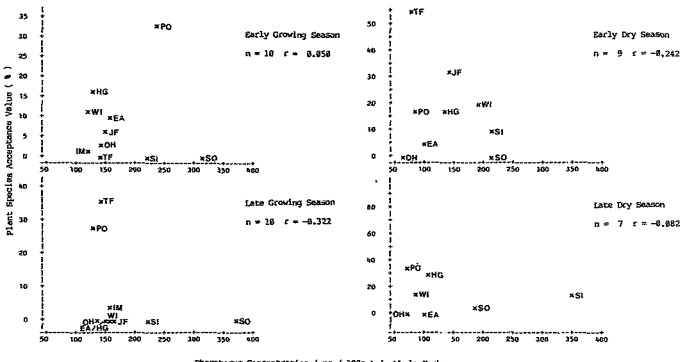


Fig 7.9. The Acceptance of Forb Species in Relation to the Concentration of Phosphorus in Whole Plants.

iii. Goats

forbesii which was low in phosphorus.

Both S. cordifolia and S. pandurae forme had above average phosphorus contents yet were of low acceptance for most of the year. Only in the late dry season was S. cordifolia of high acceptance. The other favoured plant at this time was W. indica which contained only 83 mg/100g of phosphorus on a dry weight basis.

c. Potassium

i. Kudus

The acceptance of forbs by kudus was positively correlated to the potassium content of whole forbs in the late growing and early dry season (Fig 7.10.i.). At this time the kudus had a high acceptance for J. flava and P. campestris, both of which contain high concentrations of potassium.

ii. Impalas

The impalas had a high acceptance for both J. flava and P. campestris in the early growing season (Fig 7.10.ii.). In this season alone the acceptance was significantly correlated to the potassium concentrations in forbs. In the late growing and early dry seasons the impalas had a high acceptance for T. forbesii which contains relatively little potassium.

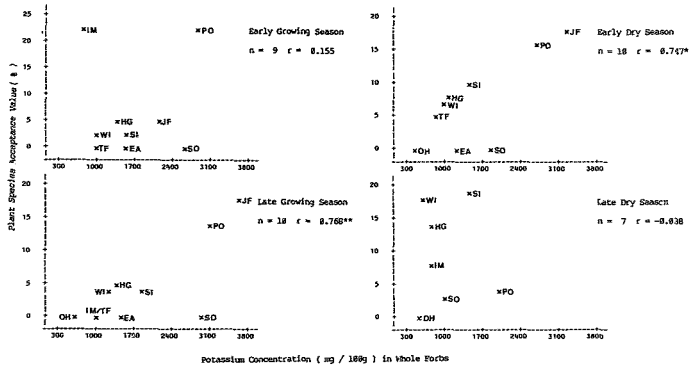


Fig 7.18. The Acceptance of Forb Species in Relation to the Concentration of Potassium in Whole Plants.

1. Rudus

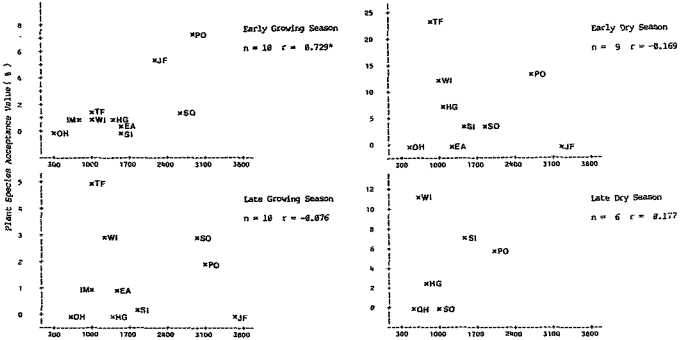


Fig 7.10. The Acceptance of Forb Species in Relation to the Concentration of Potassium in Whole Plants.

ii. Impalas

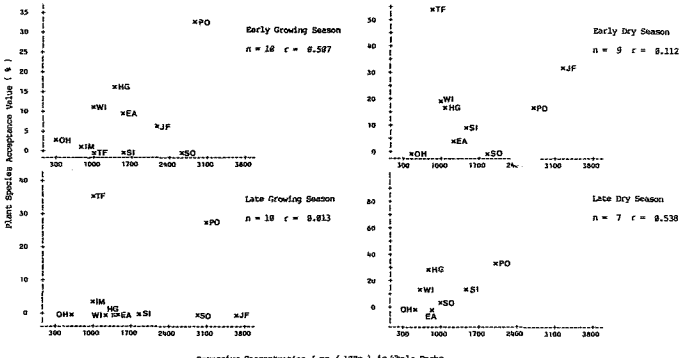


Fig 7.18. The Acceptance of Forb Species in Relation to the Concentration of Potassium in Whole Plants.

iii. Goats

iii. Goats

There was no significant correlation between the acceptance of forbs by goats and the potassium content of these plants (Fig 7.10.iii.). Like the impalas the goats also favoured T. forbesii.

iv. Plant Species Differences

J. flava and P. campestris were both rich in potassium. In the seasons when these two species were favoured a positive correlation existed between plant species acceptance and the potassium content. S. pandiraeforme was equally as rich in potassium but was generally of low acceptance. The potassium poor species T. forbesii was favoured by the impalas and goats.

d. Calcium

i. Kudus

The calcium content of forbs was significantly correlated to the acceptance by kudus in the late growing season only (Fig 7.11.i.). The correlation was mainly due to a high acceptance of J. flava which had a particularly high calcium concentration.

ii. Impalas

No significant correlation was found between the calcium content of forbs and their acceptance by impalas (Fig 7.11.ii.). The two

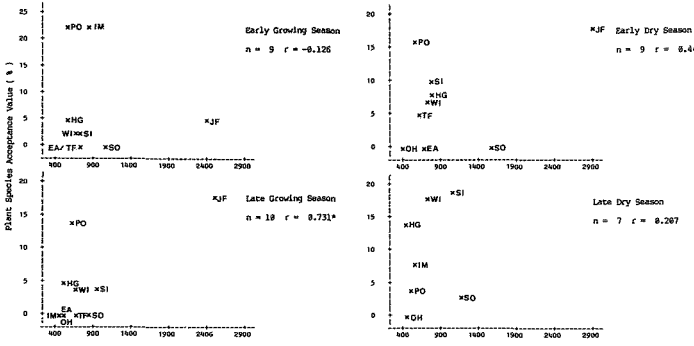


Fig 7.11. The Acceptance of Forb Species in Relation to the Concentration of Calcium in Whole Plants.

i. Kudus

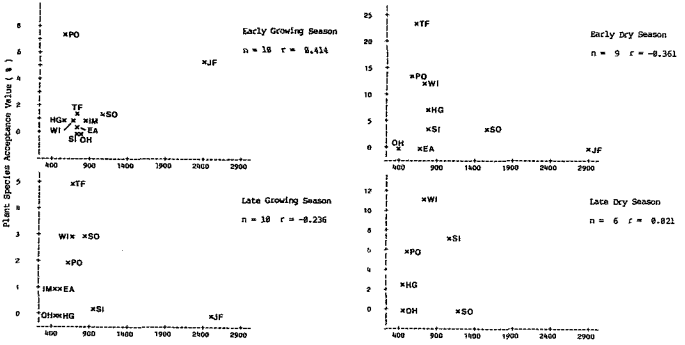


Fig 7.11. The Acceptance of Forb Species in Relation to the Concentration of Calcium in Whole Plants.

ii. Impalas

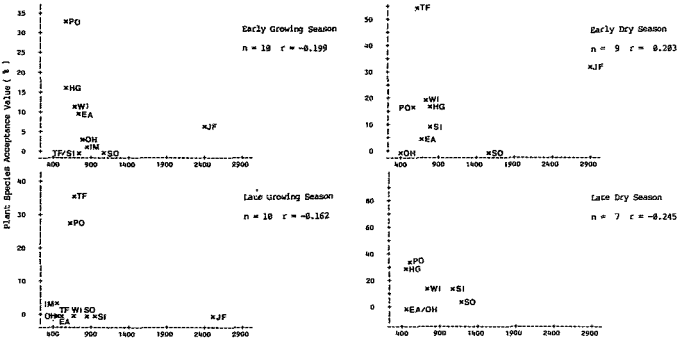


Fig 7.11. The Acceptance of Forb Species in Relation to the Concentration of Calcium in Whole Plants.

iii. Goats

species of highest calcium content were generally of low acceptance after the early growing season.

iii. Goats

As for the impalas there was no significant correlation between the acceptance of forbs by goats and the calcium content (Fig 7.11.iii.). Species of high calcium content were of low acceptance in the growing season.

iv. Plant Species Differences

J. flava was very rich in calcium as compared to the other forb species, never containing less than 2400 mg/100g dry weight. S. pandurae forme had the next highest calcium concentration but was of low acceptance. Th favoured plants P. campestris and T. forbesii were both of low calcium concentration.

e. Magnesium

i. Kudus

The magnesium content of forbs was significantly correlated to the acceptance by kudus in the late growing and early dry seasons, when these animals favoured P. campestris and J. flava, both of which were rich in magnesium (Fig 7.12.i.).

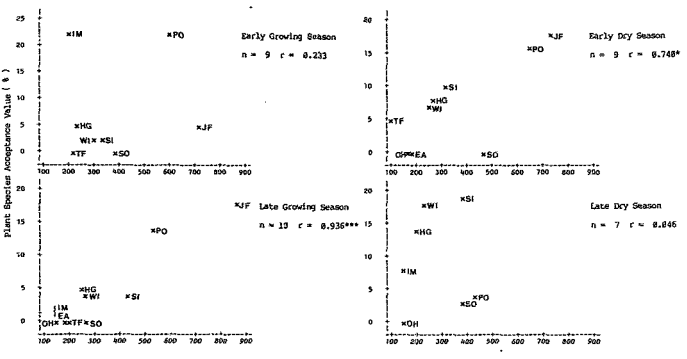


Fig 7.12. The Acceptance of Forb Species in Relation to the Concentratio.. ..gnesium in Whole Plants.

1. Xudus

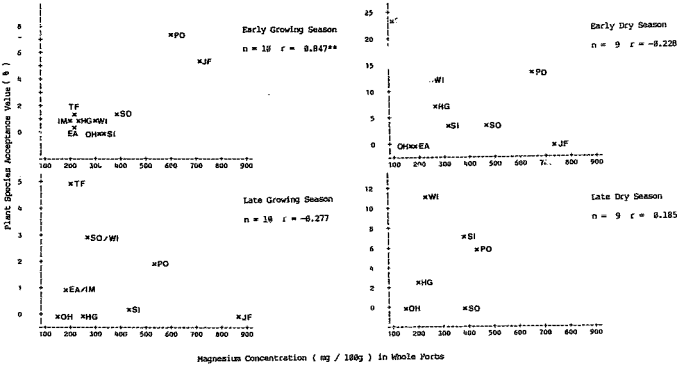


Fig 7.12. The Acceptance of Forb Species in Relation to the Concentration of Magnesium in Whole Plants.

ii. Impalas

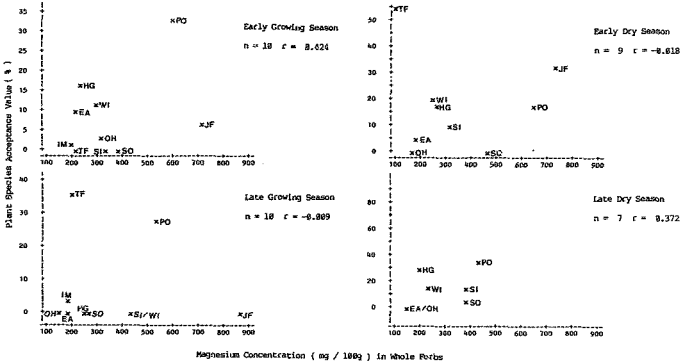


Fig 7.12. The Acceptance of Forb Species in Relation to the Concentration of Magnesium in Whole Plants.

111. Goats

ii. Impalas

The impalas had a high acceptance for the magnesium rich forbs P. campestris and J. flava in the early growing season (Fig 7.12.ii.). Acceptance was significantly correlated to magnesium content for this season only. Other favoured plants such as T. forbesii and W. indica were of low magnesium concentration.

iii. Goats

The acceptance of forbs by goats was not correlated to the magnesium content of the plants. The favoured forb species showed the full range of magnesium concentrations (Fig 7.12.iii.).

iv. Plant Species Differences

P. campestris and J. flava were rich in magnesium as compared to other forb species. T. forbesii, which was favoured by the impalas and goats had a rather low magnesium content.

f. Sodium

i. Kudus

The acceptance of forbs by the kudus was significantly correlated to the sodium content in the late growing and early dry seasons, when both P. campestris and J. flava were favoured (Fig 7.13.i.).

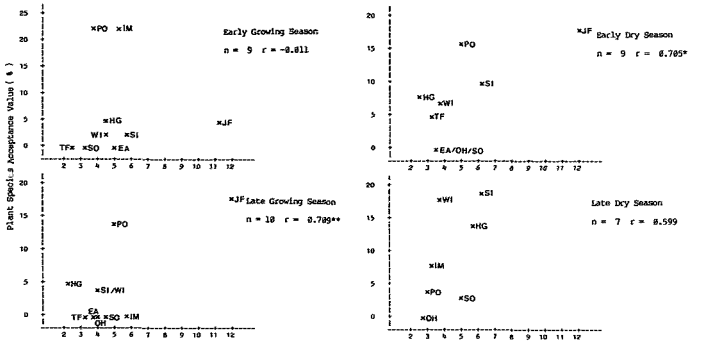


Fig 7.13. The Acceptance of Forb Species in Relation to the Concentration of Sodium in Whole Plants.

i. Kudus

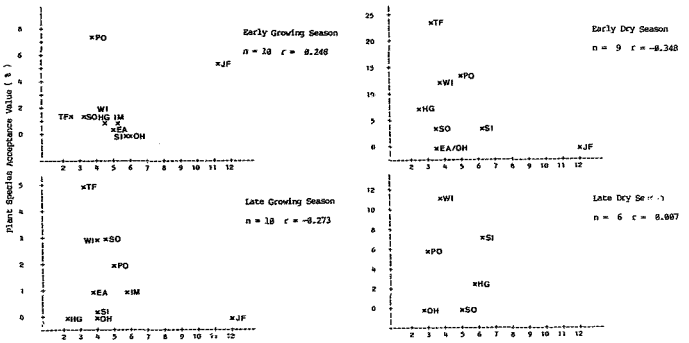


Fig 7.13. The Acceptance of Forb Species in Relation to the Concentration of Sodium in Whole Plants.

ii. Impalas

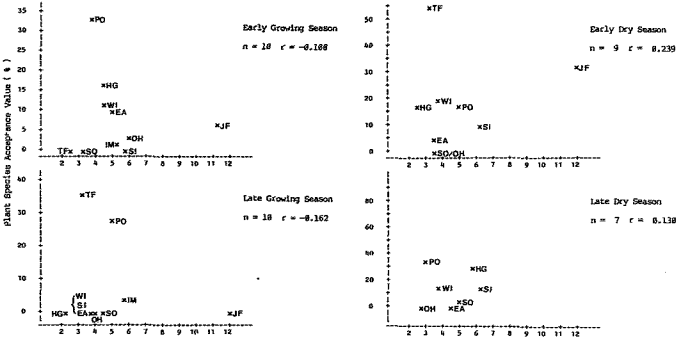


Fig 7.13. The Acceptance of Forb Species in Relation to the Concentration of Sodium in Whole Plants.

iii. Goats

ii. Impalas

The acceptance of forbs by impalas was not significantly correlated to the sodium content (Fig 7.13.ii.). Both P. campestris and J. flava were favoured in the early growing season but P. campestris was only of moderate sodium content in the preflowering phase.

iii. Goats

Goats showed no significant correlation between the acceptance of forb species and sodium concentration (Fig 7.13.iii.).

iv. Plant Species Differences

J. flava contained more sodium than the other forbs and tended to dominate the linear regressions. Once again T. forbesii was of rather low nutrient content but was a favoured species. The non-preferred plant O. herbacea was of low sodium content.

g. Moisture

i. Kudus

No significant correlation between acceptance and moisture content existed for the kudus, except in the late growing season when P. campestris and J. flava were favoured and were of relatively high

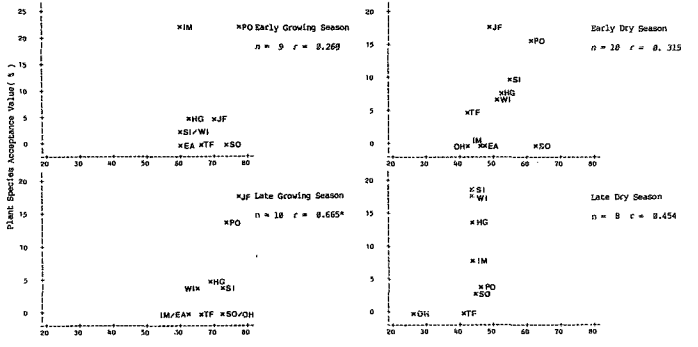


Fig 7.14. The Acceptance of Forb Species in Relation to the Concentration of Moisture in Whole Plants.

1. Kudus

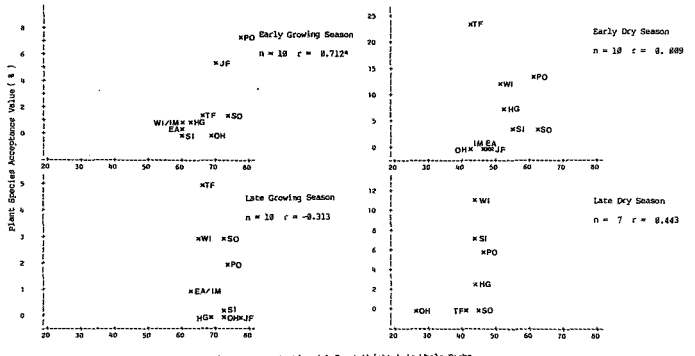


Fig 7.14. The Acceptance of Forb Species in Relation to the Concentration of Moisture in Whole Plants.

ii. Impalas

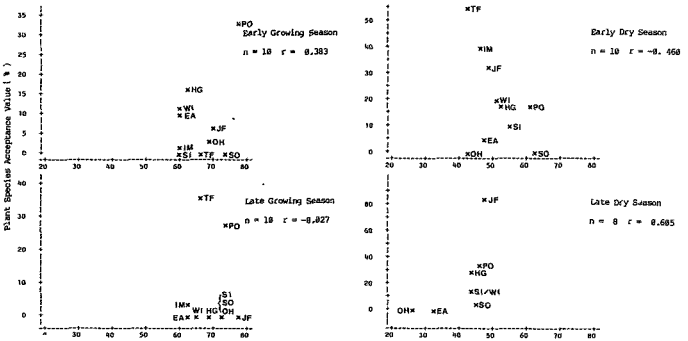


Fig 7.14. The Acceptance of Forb Species in Relation to the Concentration of Moisture in Whole Plants.

iii. Goats

moisture content (Fig 7.14.i.).

ii. Impalas

A weak positive correlation between the acceptance by impalas and the moisture content of forbs exists only in the early growing season when J. flava and P. campestris were both favoured (Fig 7.14.ii.). In the dry season the two species with lowest moisture contents were of very low acceptance.

iii. Goats

The moisture content of forbs was not correlated to their acceptance by the goats (Fig 7.14.iii.). The most favoured forbs in the growing season were of fairly high moisture content, and in the late dry season the two species of lowest moisture content were not eaten.

iv. Plant Species Differences

The plants with the highest moisture contents in the growing season were the favoured plants P. campestris and J. flava, and the non-preferred plant S. panduraeforme, E. alsinoides and O. herbacea contained least moisture, especially in the dry season and were generally of low acceptance.

h. Summary: The Acceptance of Forb Species in Relation to Nutrient Concentrations

i. The acceptance of forb species was only weakly, if at all, correlated to nutrient concentrations. Regressions were dominated by J. flava which is of very high potassium, calcium, magnesium and sodium concentration relative to other forbs. On removal of this plant from the regression no significant correlations were found.

2. Fibre

A. Woody Plants

a. Neutral Detergent Fibre (NDF)

i. Kudus

The acceptance of woody plants by kudus was not significantly correlated to the NDF content of the leaves, except in the growing season. In the early growing season the low acceptance of A. nilotica prevented the correlation from becoming significant, but there does appear to be a threshhold effect, whereby plants containing in excess of 35 - 40% NDF are of low acceptance (Fig 7.15.i.). The threshhold effect was weaker in the late growing season and non-existent by the early dry season. In the late dry season a significant negative correlation developed with the most

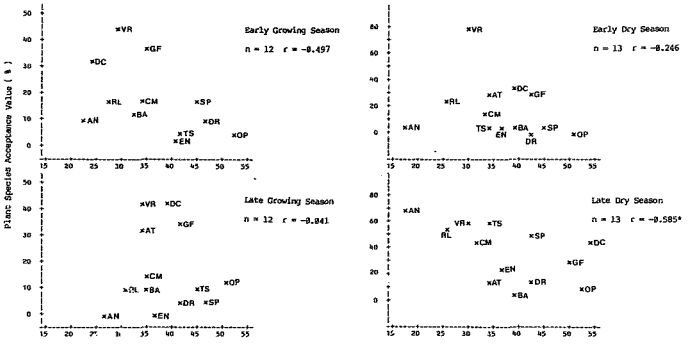


Fig 7.15. The Acceptance of Woody Plant Species in Relation to the Concentration of Neutral Detergent Fibre in the Leaves.

t. Kudus

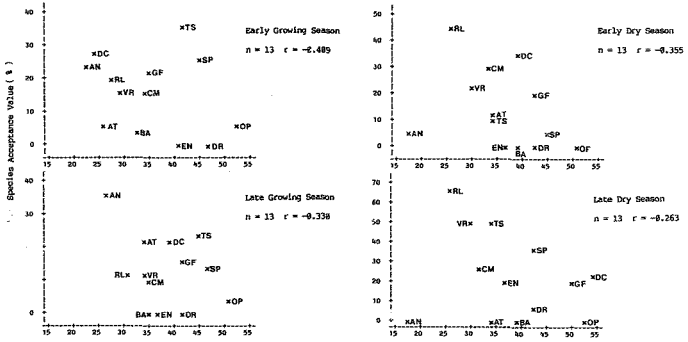


Fig 7.15. The Acceptance of Woody Plant Species in Relation to the Concentration of Neutral Detergent Fibre in the Leaves.

ii. Impalas

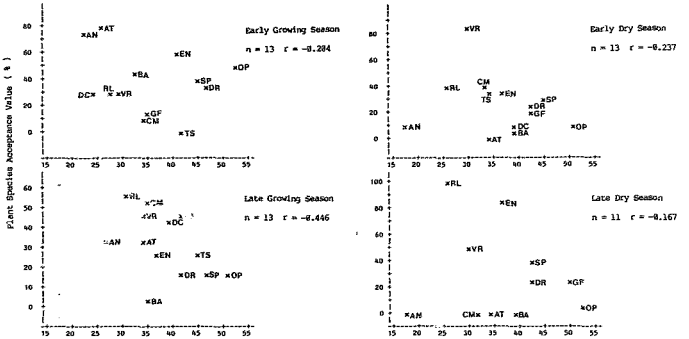


Fig 7.15. The Acceptance of Woody Plant Species in Relation to the Concentration of Neutral Detergent Fibre in the Leaves.

iii. Goats

Table 7.9. Differences Between the Neutral Detergent Fibre Concentration (% Dry Weight) in the Leaves of Favoured and Non-preferred Woody Plant Species

i. Kudus

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	30.8	± 5.4	36.5	± 8.6	10	1.134
Late Growing Season	35.0	± 5.6	40.3	± 6.9	11	1.421
Early Dry Season	34.4	± 6.5	37.3	± 9.9	11	0.562
Late Dry Season	30.5	± 8.3	44.1	± 8.0	11	2.998*

ii. Impalas

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	22.8	± 12.0	37.5	± 9.7	11	1.456
Late Growing Season	37.2	± 7.0	38.9	± 6.9	11	0.425
Early Dry Season	34.2	± 6.5	37.4	± 9.9	11	0.632
Late Dry Season	33.2	± 6.8	40.0	± 11.5	11	1.087

iii. Goats

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	34.9	± 12.2	[illegible]	± 7.7	11	0.146
Late Growing Season	34.5	± 4.8	4[illegible]	± 6.1	11	2.673*
Early Dry Season	32.0	± 4.0	40.6	± 11.2	11	1.614
Late Dry Season	33.7	± 7.1	37.9	± 11.1	10	0.680

* Significant at 95% by the Randomisation Test

favoured species being of comparatively low NDF content (Table 7.9.).

ii. Impalas

The concentration of NDF in the leaves was not significantly correlated to the acceptance of the species by impalas. There was little evidence of a threshold effect as for the kudus (Fig 7.15.ii.). In the dry season only the low acceptance for A. nilotica prevented a weak negative correlation from attaining significance (excluding A. nilotica $r = -0.619^*$ in the early dry season and $r = -0.568^*$ in the late dry season).

iii. Goats

For goats no correlation or threshhold effect between NDF content and acceptance was evident (Fig 7.15.iii.). Yet in the late growing season the preferred group of plants were of significantly lower NDF content than the non-preferrad plants (Table 7.9.). No pattern was evident in the dry season.

iv. Plant Species Differences

Four of the most fibrous woody plants O. pulchra, S. pungens, D. rotundifolia and T. sericea were generally of rather low acceptance. However, the favoured plant G. flavescens also had a high NDF content. A. nilotica was of low NDF content but was not favoured by the kudus in the growing season nor by the impalas and

goats in the dry season.

b. Acid Detergent Fibre (ADF)

i. Kudus

The ADF content of woody plant leaves was clearly significantly negatively correlated to the acceptance by kudus in the late dry season, but in the other seasons the favoured species tended to be those of intermediate ADF concentrations (Fig 7.16.i.). In the early growing season a threshold effect was evident as seen for NDF concentrations, again plants containing in excess of 35 - 40% ADF were not favoured.

ii. Impalas

For the impalas there was no correlation between plant species acceptance and ADF contents (Fig 7.16.ii.). The two species with the highest ADF contents tended to be of low acceptance to the impalas throughout the year.

iii. Goats

The goats, like the impalas, had a low acceptance for the two species rich in ADF for most of the year but other than this no selection for species low in ADF was evident (Fig 7.16.iii.).

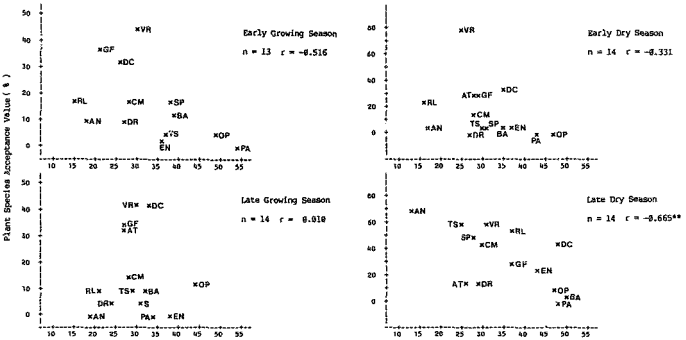


Fig 7.16. The Acceptance of Woody Plant Species in Relation to the Concentration of Acid Detergent Fibre in the Leaves.

1. Kudus

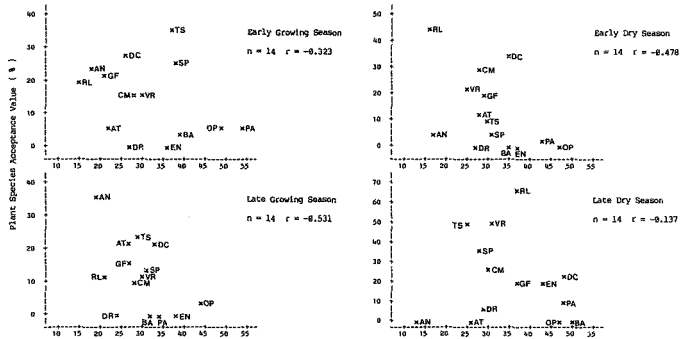


Fig 7.16. The Acceptance of Woody Plant Species in Relation to the Concentration of Acid Detergent Fibre in the Leaves.

ii. Impalas

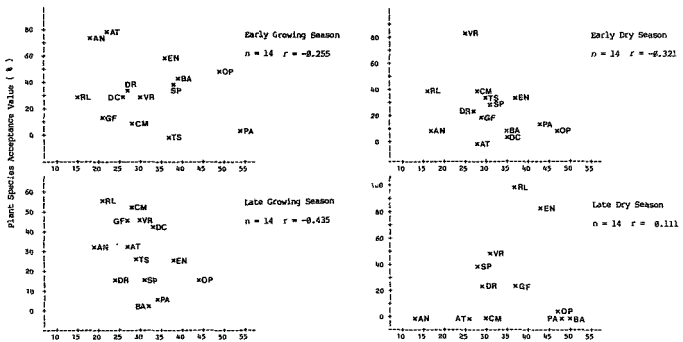


Fig 7.16. The Acceptance of Woody Plant Species in Relation to the Concentration of Acid Detergent Fibre in the Leaves.

7-30c

iii. Goats

iv. Plant Species Differences

The Acacia species, G.flavescens and R. leptodictya were relatively low in ADF and all were generally favoured by the animals. Those species containing much ADF were the non-preferred species E. natalensis, O. pulchra and P. africanum.

c. Neutral Detergent Fibre minus Acid Detergent Fibre (NDF - ADF)

i. Kudus

The acceptance of woody plants by kudus was not correlated to the NDF - ADF contents of the leaves (Fig 7.17.i.), nor was there any evidence of selection of species low in this constituent.

ii. Impalas

As for the kudus the impalas did not appear to select plant species according to the concentration of NDF - ADF in the leaves (Fig 7.17.ii.).

iii. Goats

The NDF - ADF content of the leaves of woody plants was not correlated to their acceptance by goats (Fig 7.17.iii.), although the most favoured species were often of low NDF - ADF content.

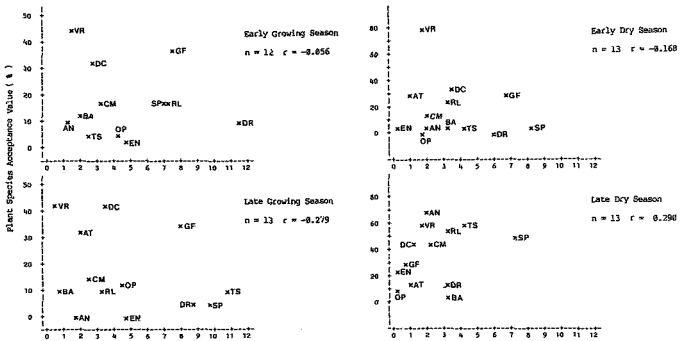


Fig 7.17. The Acceptance of Woody Plant Species in Relation to the Concentration of Neutral Detergent Fibre minus Acid Detergent Fibre in the Leaves.

1. Kudus

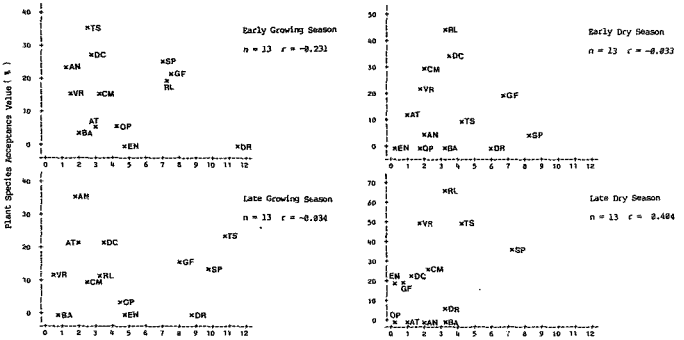


Fig 7.1. The Acceptance of Woody Plant Species in Relation to the Concentration of Neutral Detergent Fibre minus Acid Detergent Fibre in the Leaves.

ii. Impalas

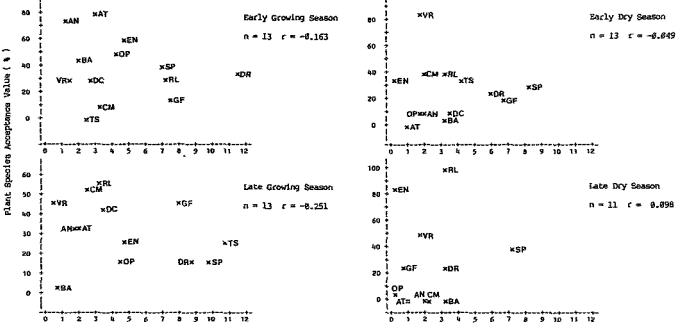


Fig 7.17. The Acceptance of Woody Plant Species in Relation to the Concentration of Neutral Detergent Fibre minus Acid Detergent Fibre in the Leaves.

111. Goats

iv. Plant species Differences

The species richest in NDF - ADF were G. flavescens, D. rotundifolia and S. pungens. These species cover a range of acceptance values. Similarly of the species low in this constituent V. rehmannii and the Acacia species were favoured while B. africana and O. pulchra were non-preferred.

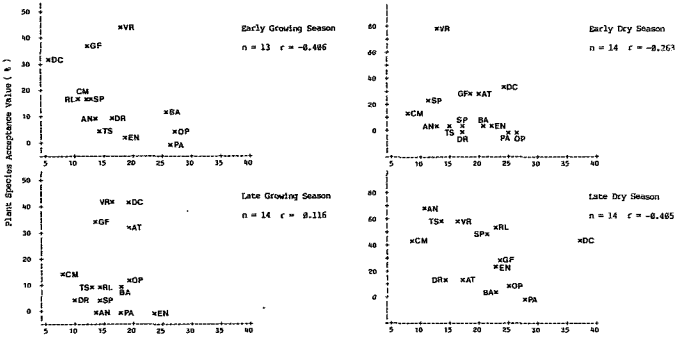
d. Acid Detergent Fibre minus Acid Detergent Lignin (ADF - ADL)

i. Kudus

The acceptance of the woody plants by kudus was not correlated to the ADF - ADL content (Fig 7.18.i.). In the dry season there was a tendency for the favoured species to be of low ADF - ADL content. This difference became significant only in the late dry season (Table 7.10.).

ii. Impalas

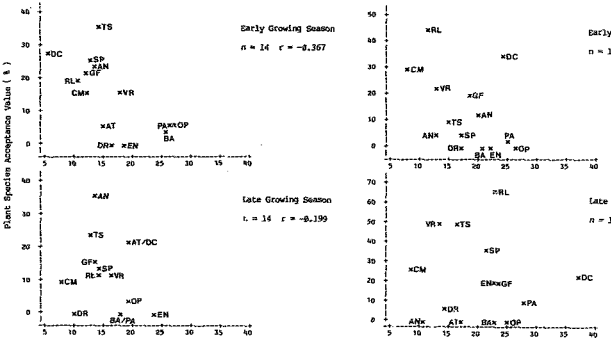
The ADF - ADL content was not correlated to the acceptance of plants by impalas (Fig 7.18.ii.). Several of the favoured species in the early growing and dry seasons were low in this constituent, but the difference between favoured and non-preferred plants was not significant (Table 7.10.).



Acid Detergent Fibre minus Acid Detergent Lignin Concentration (% Dry Weight) in Woody Plant Leaves

Fig 7.18. The Acceptance of Woody Plant Species in Relation to the Concentration of Acid Detergent Fibre minus Acid Detergent Lignin in the Leaves.

1. Kudus



Acid Detergent Fibre minus Acid Detergent Lignin Concentration (% Dry Weight) in Woody Plant Leaves

Fig 7.18. The Acceptance of Woody Plant Species in Relation to the Concentration of Acid Detergent Fibre minus Acid Detergent Lignin in the Leaves.

ii. Impalas

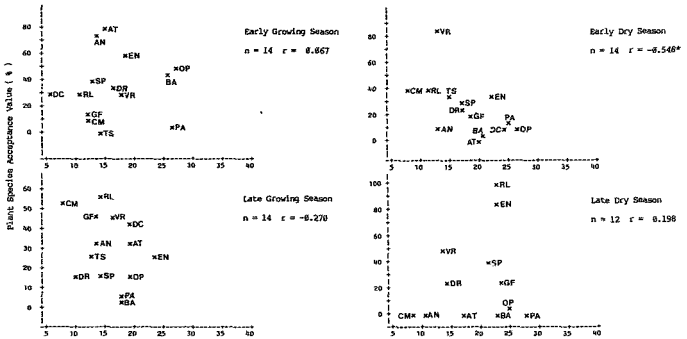


Fig 7.18. The Acceptance of Woody Plant Species in Relation to the Concentration of Acid Detergent Fibre minus Acid Detergent Lignin in the Leaves.

iii. Goats

Table 7.10. Differences Between the Acid Detergent Fibre minus Acid Detergent Lignin Concentration (% Dry Weight) in the Leaves of Favoured and Non-preferred Woody Plant Species

i. Kudus

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	15.8 ± 10.3		19.3 ± 6.3		11	0.760
Late Growing Season	16.4 ± 2.9		15.3 ± 4.8		12	0.453
Early Dry Season	17.6 ± 5.2		18.3 ± 6.0		12	0.221
Late Dry Season	16.0 ± 5.2		23.9 ± 6.3		12	2.485*

ii. Impalas

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	14.8 ± 9.2		19.9 ± 5.8		12	1.272
Late Growing Season	15.7 ± 3.3		15.7 ± 4.7		12	0.000
Early Dry Season	15.2 ± 6.9		19.7 ± 4.5		12	1.540
Late Dry Season	18.6 ± 4.0		21.3 ± 7.9		12	0.632

iii. Goats

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	19.9 ± 6.3		16.5 ± 8.3		12	0.789
Late Growing Season	15.0 ± 3.9		16.5 ± 4.5		12	0.656
Early Dry Season	14.0 ± 5.4		20.3 ± 4.4		12	2.385*
Late Dry Season	20.2 ± 4.2		19.2 ± 6.4		10	0.289

* significant at 95% by the Randomisation Test

iii. Goats

A significant negative correlation existed between the ADF - ADL content of woody plants and their acceptance by goats only in the early dry season (Fig 7.18.iii.). Other than this no pattern existed.

iv. Plant Species differences

The favoured plant D. cinerea was relatively rich in ADF-ADL, while plants low in this type of fibre showed a variety of acceptance values.

e. Acid Detergent Lignin minus Acid Detergent Ash (ADL - Ash)

i. Kudus

The acceptance of plant species by kudus was only significantly negatively correlated to the ADL content in the late dry season (Fig 7.19.i.), but the group of plants favoured in the late growing and early dry seasons were of significantly lower ADL content than the group of less preferred species (Table 7.11.).

ii. Impalas

The acceptance of woody plants by impalas was not significantly correlated to the ADL content (Fig 7.19.ii.). Some of the favoured species in the late growing and dry seasons were of low ADL

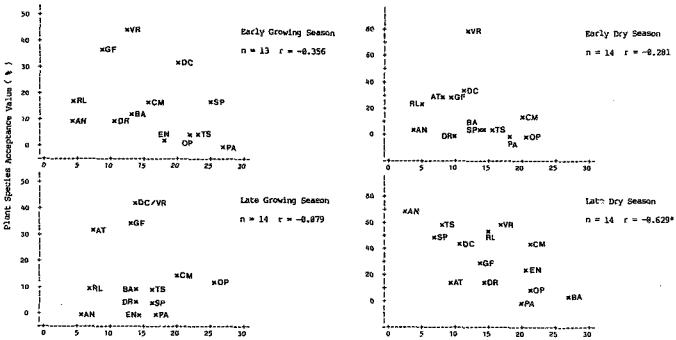


Fig 7.19. The Acceptance of Woody Plant Species in Relation to the Concentration of Acid Detergent Lignin minus Acid Detergent Ash in the Leaves.

I. Kudus

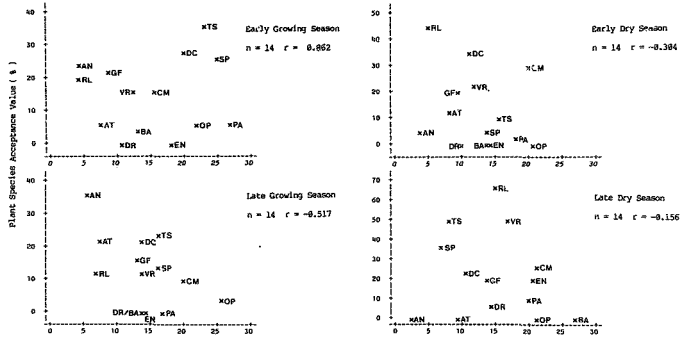


Fig 7.19. The Acceptance of Woody Plant Species in Relation to the Concentration of Acid Detergent Lignin minus Acid Detergent Ash in the Leaves.

ii. Impalas

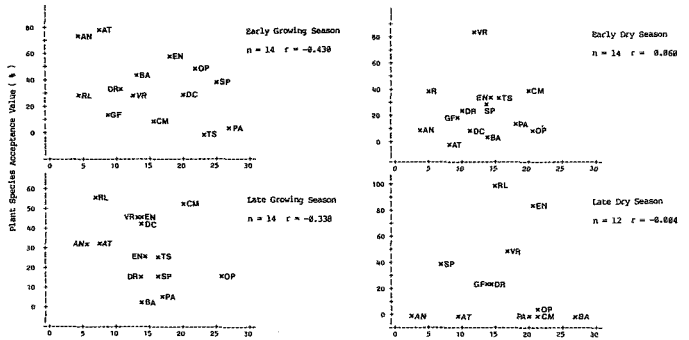


Fig 7.19. The Acceptance of Woody Plant Species in Relation to the Concentration of Acid Detergent Lignin minus Acid Detergent Ash in the Leaves.

iii. Goats

Table 7.11. Differences Between the Acid Detergent Lignin minus Ash Concentration (% Dry Weight) in the Leaves of Favoured and Non-preferred Woody Plant Species

i. Kudus

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	14.1	± 8.6	16.8	± 7.4	11	0.571
Late Growing Season	10.8	± 3.9	15.9	± 5.0	12	2.365*
Early Dry Season	9.1	± 2.7	14.4	± 5.1	12	2.119*
Late Dry Season	11.9	± 6.6	16.8	± 6.0	12	1.442

ii. Impalas

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	14.3	± 9.7	15.8	± 6.4	12	0.352
Late Growing Season	11.2	± 4.5	15.7	± 5.0	12	1.644
Early Dry Season	11.4	± 5.5	13.1	± 5.0	12	0.590
Late Dry Season	11.7	± 4.7	15.9	± 6.9	12	0.940

iii. Goats

	Favoured		Non-Preferred			
	Mean	SE	Mean	SE	df	t
Early Growing Season	13.1	± 7.3	16.3	± 8.0	12	0.738
Late Growing Season	11.5	± 5.1	16.7	± 4.0	12	2.188*
Early Dry Season	13.2	± 5.6	12.1	± 5.0	12	0.379
Late Dry Season	14.8	± 5.8	15.9	± 7.3	10	0.258

* Significant at 95% by the Randomisation Test

content, but as a group, the favoured species were not significantly different from non-favoured plants (Table 7.11.).

iii. Goats

No significant correlation existed between the ADL content of plants and their acceptance to goats (Fig 7.19.iii.). However, the species favoured in the late growing season were of significantly lower ADL content than the non-preferred plants (Table 7.11.).

iv. Plant Species Differences

A. nilotica and R. leptodictya were of low ADL content but were not of high acceptance to the kudus until the late dry season. The ADL rich species O. pulchra, P. africanum, T. sericea and S. pungens were mainly of low to intermediate acceptance.

f. Summary: The Acceptance of Woody Plant Species in Relation to Fibre Concentration

i. The acceptance of woody plants by browsing ungulates was not strongly correlated to fibre content. NDF, ADF and ADL had a greater effect on acceptance than did NDF - ADF or ADF - ADL.

ii. In the early growing season acceptance was not correlated to fibre content, but for the kudus, there was a threshhold effect whereby plants containing in excess of 35 - 40% NDF or ADF were of low acceptance.

iii. Woody species favoured in the late growing season tended to be of low ADL content. Species favoured by the kudus and goats contained significantly less ADL than the non-preferred plants; for impalas the differences were not quite significant. The plants favoured by the goats were also of significantly lower NDF content than less preferred plants. Neither NDF - ADF or ADF - ADL concentrations affected the acceptance of woody plant species in this season.

iv. In the early dry season the plants favoured by the kudus were lower in ADL than the non-preferred species. Several of the species preferred by the impalas and goats were of low NDF content but on average there was not a significant difference between preferred and non-preferred groups of plants. The goats also favoured those species low in ADF - ADL.

v. For the kudus only acceptance in the late dry season was negatively correlated to both NDF and ADL contents. The favoured plants were also significantly lower in ADF - ADL than non-preferred species. In this season the impalas also favoured those species with low NDF contents, but for the goats no significant relationship between acceptance and fibre content was evident.

vi. Plants of high concentrations of NDF or its components ADF or ADL were generally of low acceptance to browsing ungulates, but plants with a relatively high concentration of NDF - ADF

or ADF - ADL showed a range of values.

B. Forbs

a. Neutral Detergent Fibre (NDF)

i. Kudus

The NDF content of whole forb plants was not significantly correlated to the acceptance by kudus (Fig 7.20.i.). Several species of high acceptance in the dry and early growing seasons were of high NDF content.

ii. Impalas

Impalas showed a similar lack of correlation between acceptance and NDF content (Fig 7.20.ii.). They often favoured species with high NDF contents.

iii. Goats

The NDF content of forbs was not significantly correlated to the acceptance by goats (Fig 7.20.iii.). At all times of year NDF rich plants were often favoured.

iv. Plant Species Differences

P. campestris, I. macra and T. forbesii were all of high NDF

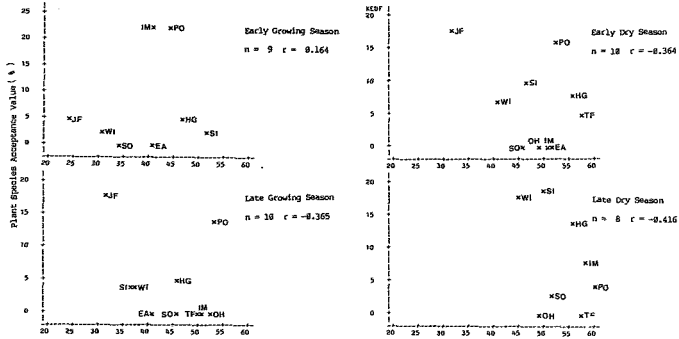


Fig 7.20. The Acceptance of Forb Species in Relation to the Concentration of Neutral Detergent Fibre in Whole Plants.

1. Kudus

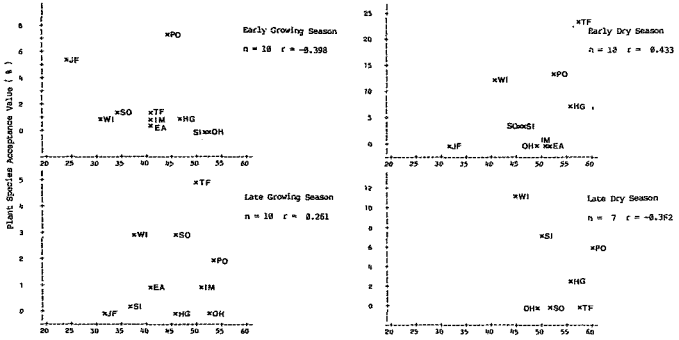


Fig 7.26. The Acceptance of Forb Species in Relation to the Concentration of Neutral Detergent Fibre in Whole Plants.

ii. Impalas

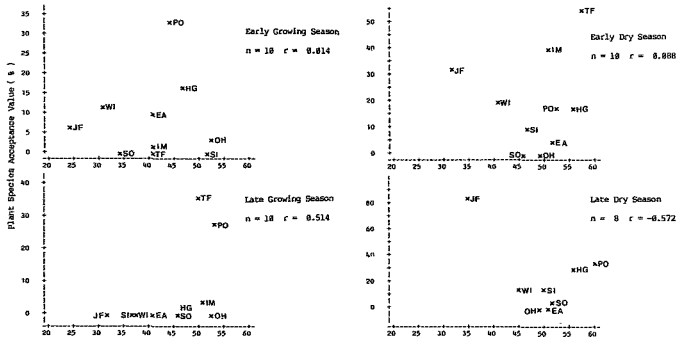


Fig 7.28. The Acceptance of Forb Species in Relation to the Concentration of Neutral Detergent Fibre in Whole Plants.

iii. Goats

content yet were favoured at certain times of year. W. indica had a relatively low NDF content but was eaten mainly in the late dry season.

b. Acid Detergent Fibre (ADF)

i. Kudus

Forb species favoured by the kudus tended to be of moderate to low ADF concentration but overall there was no signifiant correlation between acceptance and ADF content (Fig 7.21.i.).

ii. Impalas

The acceptance of forb species was not correlated to the ADF content of the plants (Fig 7.21.ii.). In the early growing season the two most favoured species were of low ADF concentration, but for the rest of the year the favoured plants were often of high ADF content.

iii. Goats

In the late growing season and early dry season the goats favoured two species high in ADF, but in the late dry season a negative correlation developed between ADF concentration and acceptance. This was due to the high acceptance value of J. flava which contains much less ADF than the other forb species (Fig 7.21.iii.).

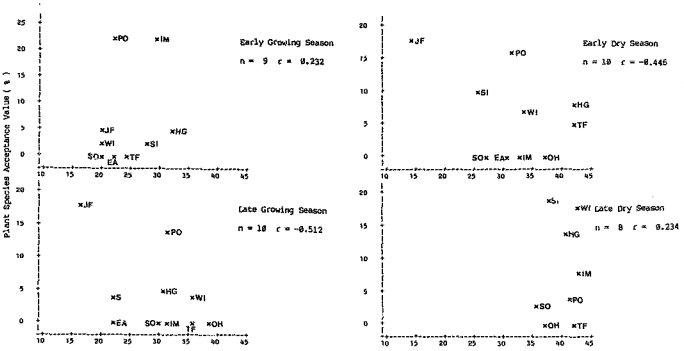


Fig 7.21. The Acceptance of Forb Species in Relation to the Concentration of Acid Detergent Fibre in Whole Plants.

1. Kudus

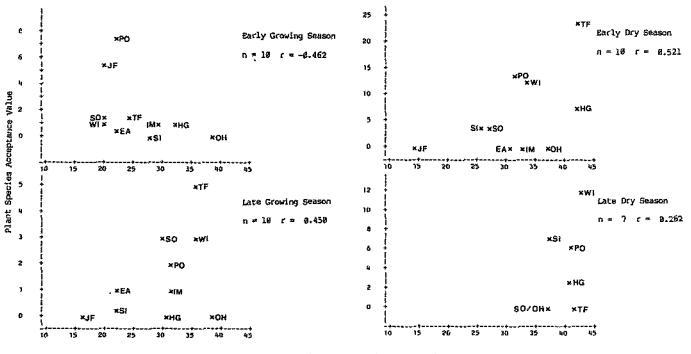


Fig 7.21. The Acceptance of Forb Species in Relation to the Concentration of Acid Detergent Fibre in Whole Plants.

ii. Impalas

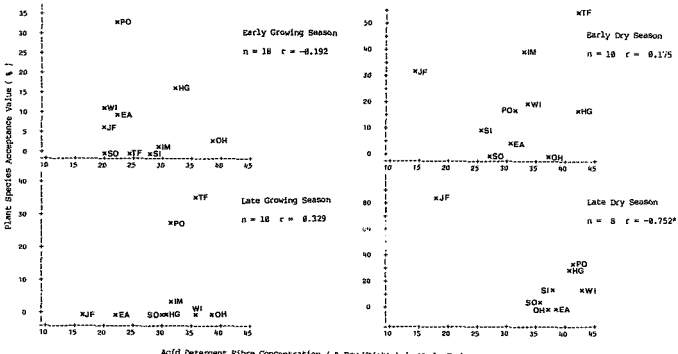


Fig 7.21. The Acceptance of Forb Species in Relation to the Concentration of Acid Detergent Fibre in Whole Plants.

iii. Goats

iv. Plant Species Differences

J. flava contained relatively less ADF than most other forb species but the acceptance of this plant varied widely between animals and between seasons. Plants rich in ADF included the favoured T. forbesii as well as non-preferred species such as O. herbacea.

c. Neutral Detergent Fibre minus Acid Detergent Fibre (NDF - ADF)

i. Kudus

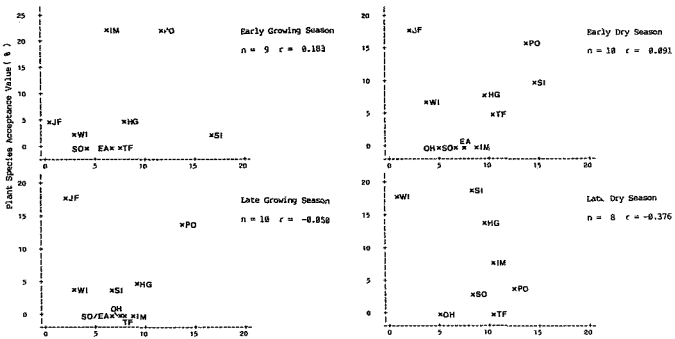
There was no correlation between the acceptance of forb species by kudus and the concentration of NDF - ADF in the plants (Fig 7.22.i.).

ii. Impalas

The impalas like the kudus, showed no correlation between acceptance of forbs and NDF- ADF concentrations (Table 7.21.ii.). Favoured species showed a wide range of fibre contents

iii. Goats

Once again there was no significant relationship between forb species acceptance and NDF - ADF contents. In the late growing season the favoured species were rich in this fibre component.



Neutral Detergent Fibre minus Acid Detergent Fibre Concentration (% Dry Weight) in Whole Forbs

Fig 7.22. The Acceptance of Forb Species in Relation to the Concentration of Neutral Detergent Fibre minus Acid Detergent Fibre in Whole Plants.

i. Kudus

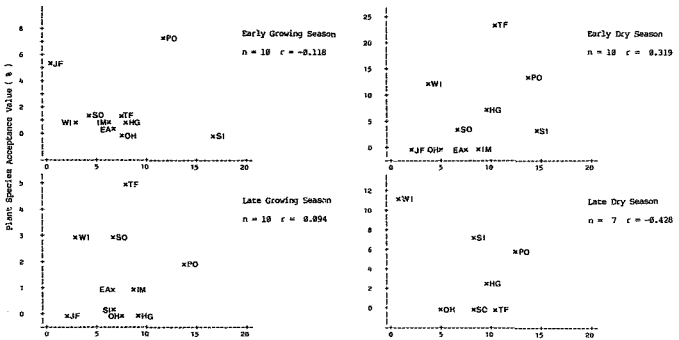


Fig 7.22. The Acceptance of Forb Species in Relation to the Concentration of Neutral Detergent Fibre minus Acid Detergent Fibre in Whole Plants.

11. Impalas

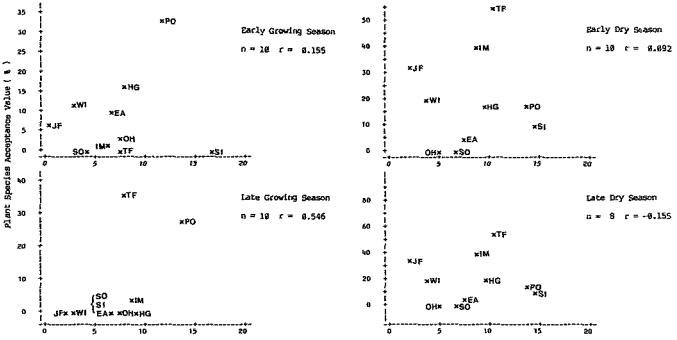


Fig 7.22. The Acceptance of Forb Species in Relation to the Concentration of Neutral Detergent Fibre minus Acid Detergent Fibre in Whole Plants

iii. Goats

iv. Plant Species Differences

P. campestris was comparatively rich in NDF - ADF and was a favoured species. J. flava and W. indica were low in this type of fibre but were only favoured at certain times of year.

d. Acid Detergent Fibre minus Acid Detergent Lignin (ADF - ADL)

i. Kudus

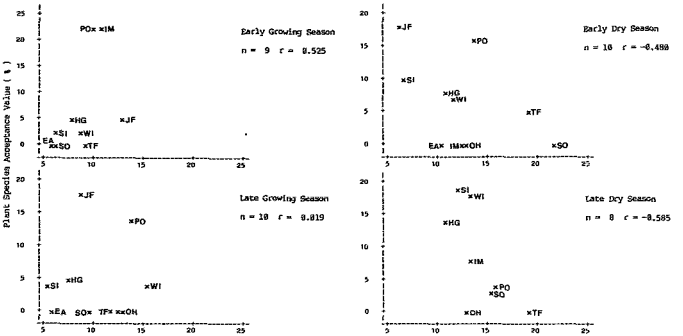
The acceptance of forbs by kudus was not significantly correlated to the ADF - ADL content (Fig 7.23.i.). The most highly favoured species were of moderate ADF - ADL content.

ii. Impalas

No signifcant correlation was found between the acceptance of forbs by impalas and the ADF - ADL content (Fig 7.23.ii.). Several species favoured in the early dry season were of high ADF - ADL content, while species low in this fibre were often not favoured.

iii. Goats

The goats also showed no significant correlation between ADF - ADL content and the acceptance of forbs (Fig 7.23.iii.). In the late wet season several favoured species were of high ADF - ADL content. Only in the late dry season were some of the species low in this fibre favoured.



Acid Detergent Fibre Minus Acid Detergent Lignin Concentration (% Dry Weight) in Whole Forbs

Fig 7.23. The Acceptance of Forb Species in Relation to the Concentration of Acid Detergent Fibre minus Acid Detergent Lignin in Whole Plants.

1. Exlus

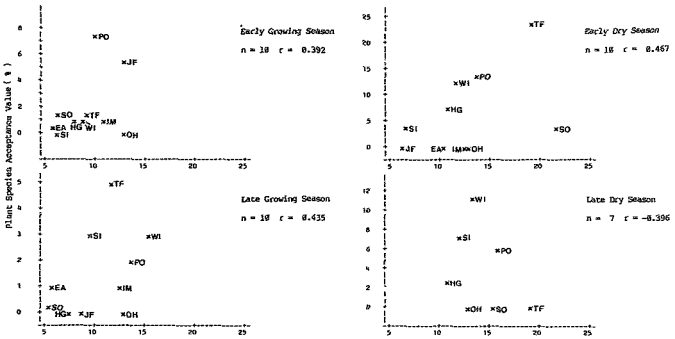


Fig 7.23. The Acceptance of Forb Species in Relation to the Concentration of Acid Detergent Fibre minus Acid Detergent Lignin in Whole Plants.

ii. Impalas

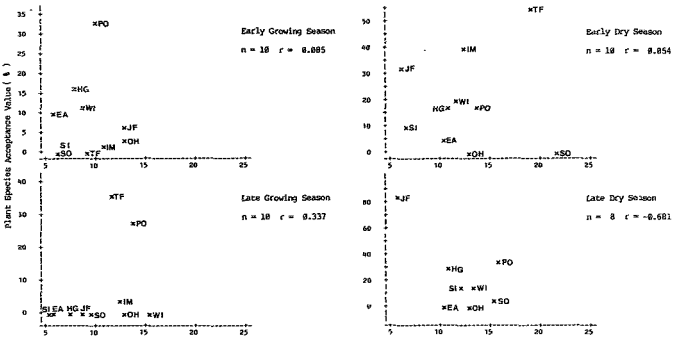


Fig 7.23. The Acceptance of Forb Species in Relation to the Concentration of Acid Detergent Fibre minus Acid Detergent Lignin in Whole Plants.

iii. Goats

iv. Plant Species Differences

P. campestris and O. herbacea were the two species of highest ADF - ADL content but were at opposite ends of the acceptance spectrum.

e. Acid Detergent Lignin minus Acid Detergent Ash (ADL - Ash)

i. Kudus

There was a negative correlation between ADL content and the acceptance of forbs in the late growing season. This was mainly caused by a high acceptance for both J. flava and P. campestris (Fig 7.24.i.). Species favoured in the early dry season tended to be of low ADL content, but the difference between preferred and non-preferred groups of species was not significant. In the late dry season several ADL rich species were favoured.

ii. Impalas

There was a significant negative correlation between acceptance by impalas and the ADL content of forbs in the early growing season (Fig 6.24.ii.). This was due to the high acceptance of P. campestris and J. flava. Several species favoured in the late dry season had high ADL contents.

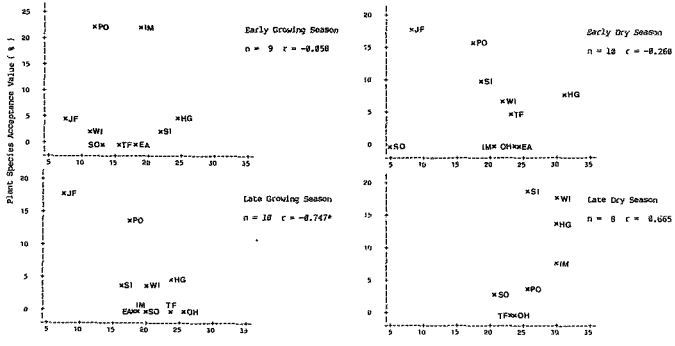


Fig 7.24. The Acceptance of Forb Species in Relation to the Concentration of Acid Detergent Lignin minus Acid Detergent Ash in Whole Plants.

1. Kudus

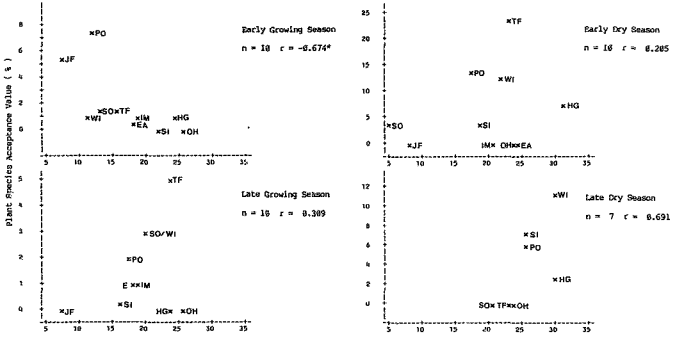
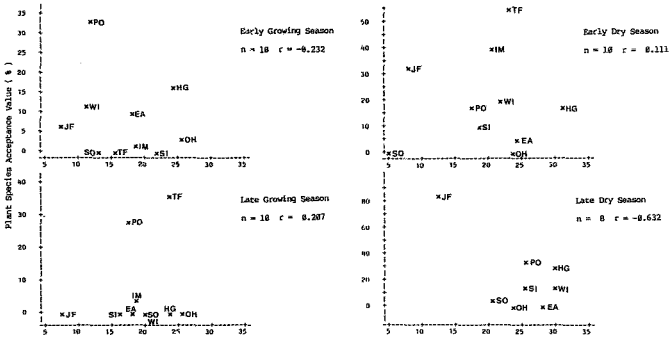


Fig 7.24. The Acceptance of Forb Species in Relation to the Concentration of Acid Detergent Lignin minus Acid Detergent Ash in Whole Plants.

ii. Impalas



Acid Detergent Lignin Concentration (% Dry Weight) in Whole Forbs

Fig 7.24. The Acceptance of Forb Species in Relation to the Concentration of Acid Detergent Lignin minus Acid Detergent Ash in Whole Plants.

iii. Goats

iii. Goats

No significant correlation existed between the acceptance of forbs by goats and concentrations of ADL (Fig 7.24.iii.). The most favoured forb plants in the *early growing and late dry seasons* were of low ADL content, but in the other seasons species of moderate ADL content were favoured.

iv. Plant Species Differences

P. Campestris and J. flava were of low ADL content in the growing season. When both were of high acceptance a *negative correlation* developed between ADL and acceptance. The perennial plants were of increased acceptance in the late dry season and contained more ADL than the less stemmy species favoured in the growing season.

f. Summary: The Acceptance of Forb Species in Relation to Fibre Content

i. The acceptance of forbs by browsing ungulates was not determined by the fibre content of whole plants.

ii. Only ADL showed a significant negative relationship with accepance, and then only for impalas and kudus in the growing season.

iii. In the late dry season fibrous perennial forbs increased in acceptance as little else was available.

3. Toxins

A. Woody Plants

a. Mono- and Sesqui- Terpenes

Low molecular weight terpenes were detected in the leaves of all woody plants and it was not possible to quantify or distinguish between mono- and sesqui-terpenes. However, an aromatic odour is characteristic of mono-terpenes. Hence highly aromatic plants were presumed to be richer in these compounds than non-aromatic plants.

i. Kudus

The aromatic species V. rehmannii was favoured through out the year by the kudus, but the other common aromatic woody species R. leptodictya was of low acceptance in all but the late dry season.

ii. Impalas

Both aromatic woody species were of low acceptance to the impalas in the growing season, but were favoured in the dry season.

iii. Goats

The goats had a high acceptance of the two aromatic woody plants in all but the early growing season.

iv. Plant Species Differences

V. rehmannii and R. leptodictya were the most common aromatic woody plants. Other aromatic woody plants were the less common V. mombassae and R. pyroides. R. pyroides was of high acceptance to all three animal species, V. mombassae was very rare and was only seen to be eaten by the kudus.

b. Saponins

i. Kudus

The kudus had a low acceptance for the mature foliage of the four woody plant species showing high levels of foaming activity, indicative of saponins, and confirmed by TLC. Plants containing little or no foaming activity were of varied acceptance to kudus.

ii. Impalas

With the exception of T. sericea the impalas had a low acceptance of all species with a high to intermediate foaming activity. Again those species with little or no foaming activity were of varied acceptance.

iii. Goats

The goats did not favour three of the species which foamed most

vigorously when shaken in an aqueous alcoholic solution, but had a high acceptance for R. leptodictya.

iv. Plant Species Differences

The extracts of mature leaves of B. africana, P.africanum, R. leptodictya and T. sericea foamed vigorously in solution, yet little foaming was observed for the immature foliage. Species containing little saponins (by foam and TLC) were the armed species, evergreen species, and G. flavescens and D. rotund se plants show a wide variety of acceptance values. The ess common species C. bispinosa and Vangueria infaustra are reported to contain saponins (Watt and Breyer-Brandwijk 1962). The evergreen C. bispinosa was of fairly high acceptance in the dry season, especially to the impalas and goats, but V. infaustra was not favoured.

c. Alkaloids

i. Kudus

The kudus had a low acceptance for S. pungens in all but the late dry season. This species gave a consistent reaction with alkaloid detection reagents. The only other woody plant species to give a consistent, although very weak, reaction was the favoured plant V. rehmannii. Alkaloids were detected in the immature leaves of D. rotundifolia and T. sericea. The kudus ate the new leaves of D. rotundifolia more readily than the mature leaves despite the

possible presence of alkaloids. T. sericea was of low acceptance in the growing season.

ii. Impalas

Impalas favoured neither V. rehmannii or S. pungens in the growing season, but ate both species in the dry season. Young leaves of both T. sericea and D. rotundifolia were eaten.

iii. Goats

The patterns of acceptance by goats for the woody plants possibly containing alkaloids was very similar to that of the kudus, with no evidence of avoidance of alkaloids.

iv. Plant Species Differences

Few of the woody plant species tested reacted with the alkaloid detection reagents. S. pungens gave a stronger reaction than V. rehmannii which was generally of higher acceptance to the animals. The presence of alkaloids in the new leaves of T. sericea and D. rotundifolia did not relate to the patterns of acceptance of these species.

d. Cyanogenic Glycosides

No cyanogenic activity was detected in the leaves of woody plants.

The impalas in particular spent much time eating the pods of A. tortilis, which are sometimes reported as having cyanogenic activity but the A. tortilis pods at Nylsvley were not analysed.

Mundulea sericea is also reported to contain cyanogenic glycosides but was seen to be eaten occasionally by the impalas and goats.

e. Other Toxins

i. Toxic Glucosides

T. sericea is reported to contain a toxic glucoside 'Nerifolin' in the leaves. The very new and waxy leaves of T. sericea were not eaten but the impalas had a moderately high acceptance of these leaves once they reached full size. The kudus and goats had a lower acceptance of this species.

ii. Monofluoroacetate

The woody geophyte Dichapetalum cymosum produces new green leaves in the late dry season in advance of most other plants. These new leaves contain high levels of monofluroacetate, a lethal heart toxin. The impalas and kudus ignored these new leaves and were not even seen to sniff them. The goats, however, did eat this plant and one animal died as a consequence. When new D. cymosum leaves were present the goats had to be kept in a paddock cleared of this plant. During feeding trials when they were out in the main

enclosure, the goats had to be physically restrained from eating the toxic leaves.

iii. Terpenes, Steroids and Latex

Both Croton gratissimus and Ozoroa paniculosa contained a white terpenoid latex. C. gratissimus was rare but was seen to be eaten by the kudus. O. paniculosa was more common and was of low acceptance to the kudus and impalas, but was favoured in all seasons by the goats.

Steroids are triterpenes and are reported in the rare woody species V. infaustra which was not eaten by the kudus and impalas, and in C. bispinosa which was of high acceptance to impalas and goats in the dry season but of rather low acceptance to kudus.

f. Unidentified Toxins

Securidaca longipedunculata is highly poisonous to man, being used for 'trial by ordeal' in initiation ceremonies (Watt and Breyer-Brandwijk 1962). It was, however, of moderate acceptance to all three species of browsing ungulates.

g. Summary: The Acceptance of Woody Plant Species in Relation to the Presence of Toxins

i. Plant species acceptance was not influenced by the presence of alkaloids or aromatic compounds.

ii. Cyanogenic activity was absent from the woody plant species tested.

iii. Plants with a high level of foaming activity in solution, indicative of saponins, tend to be of low acceptance.

iv. The impalas and kudus avoided Dichapetalum cymosum, containing the lethal toxin monofluoroacetate. The goats ate this plant and were duly poisoned.

B. Forbs

a. Mono- and Sesqui- Terpene Lactones

All the common forbs tested contained low molecular weight terpenes but none were aromatic.

i. Kudus

The kudus favoured several species of aromatic forbs including Lippea javanica, Lantana rugosa and Ocimum canum. They also had a high acceptance for the compositae species Vernonia oligocephala. Unlike many other members of this family V. oligocephala does not contain toxic sesquiterpenes.

ii. Impalas

The impalas also ate V. oligocephala and favoured L. javanica, L. rugosa and several members of the aromatic labiate family, especially O. canum and Becium angustifolium.

iii. Goats

The goats had a high acceptance of B. angustifolium but rarely encountered other aromatic forbs.

iv. Plant Species Differences

Most aromatic forbs belonged to the Labiatae and Verbenaceae and were often eaten when encountered by the animals.

b. Saponins

i. Kudus

The kudus had a low acceptance for the two forbs found to contain saponins in the pre-flowering phase. All the forbs analysed seemed to contain saponins in the late growing season. No selection for those species free of saponins in the dry season was evident. Aloes also contain saponins but were eaten by the kudus.

ii. Impalas

As for the kudus, the pattern of acceptance of forbs by impalas did not appear to be influenced by the presence of saponins, except that the acceptance of the two species containing saponins in the pre-flowering stage was low.

iii. Goats

The acceptance of forb species to goats did not seem to be affected by the presence of saponins. Like the kudus and impalas, the goats had a low acceptance of the two species containing saponins in the pre-flowering phase of the two flowering phase.

iv. Plant Species Differences

Saponins were detected only in the perennial species H. grisea and S. cordifolia in the early growing season. Neither of these species were favoured at this time of year. All the forbs reacted with saponin detection reagents in the late growing season. P. campestris, J. flava and S. pandurae forme ceased to react with the saponin detection reagents in the dry season. These species show a variety of acceptance values.

c. Alkaloids

i. Kudus

The kudus had a high acceptance of one of the forb species giving a strong reaction with alkaloid detection reagents, but a low acceptance for the other two species giving a similar reaction. The only forb not reacting with the reagent, W. indica, was of low acceptance in the growing season, but more favoured in the dry season.

ii. Impalas

The impalas showed no consistent pattern of acceptance for species reacting strongly with alkaloid detection reagents. The one alkaloid free forb was only of high acceptance in the dry season.

iii. Goats

The goats also favoured one of the strongly reacting species, but had a low acceptance of the other species. As for impalas, W. indica was of low acceptance in the growing season, but the acceptance increased in the dry season.

iv. Plant Species Differences

J. flava and to a slightly lesser extent S. panduraeforme and T. forbesii reacted strongly to the alkaloid detection reagents. S.

pandurae*f*orme was a non-preferred species but the other two were favoured for limited periods. The only plant not to react with Mayer's or Dragendorff's reagents was W. indica, but this species was not favoured in the growing season.

d. Cyanogenic Glycosides

The only common forb to contain cyanogenic glycosides was J. flava. Cyanogenesis was only detected in the pre-flowering plants. The kudus and goats did not have a high acceptance for this plant at this time of year, but for the impalas the pre-flowering plants were of higher acceptance than older, non-cyanogenic plants.

Cyanogenic activity is reported for some species of Commelina and Tephrosia. In this study T. forbesii was a favoured forb and no cyanosis was detected. Commelina species were also favoured by the animals.

e. Other Toxins

i. Specific Alkaloids

The Kalanchoe species contain a highly neurotoxic alkaloid 'Cotyledontoxin' (Watt and Breyer-Brandwijk 1962). These plants were avoided by the impalas and kudus but were eaten by the goats in the growing season, when there was plenty of alternative food available. One of the goats showed classic symptoms of cotyledontoxin poisoning for several weeks.

The goats, but not the kudus and impalas, also ate Nidorella resedifolia which contains a toxic alkaloid. Although some Solanum species have highly toxic fruit containing solanine and solanidine the common species at Nylsvley, S. panduraeforme, was not toxic, but was only of moderate acceptance to the impalas and of lower acceptance to the kudus and goats.

ii. Cardiac Glycosides

Asclepias species contain toxic cardiac glycosides. They were avoided by the impalas and kudus but eaten by the goats.

iii. Terpenes and Steroids

Diterpenes are reported to occur in L. rugosa, Labiate species and Clerodendron species. All were eaten by the ungulates. Steroids occur in W. indica and Elephantorrhiza obliqua. Although W. indica was favoured only in the late dry season, E. obliqua was of high acceptance in the growing season.

iv. Oxalates

Oxalis corniculatus and Portulaca quadrifida contain oxalates. Neither species was preferred.

f. Summary: The Acceptance of Forb Species in Relation to the Presence of Toxins

i. Other than the avoidance of a few highly poisonous forbs, selection by browsing ungulates did not appear to be related to the presence of toxins.

ii. The indigenous kudus and impalas avoided highly toxic forbs such as the Kalanchoe and Asclepias species which contain the neurotoxin 'Cotyledontoxin' and cardiac glycosides respectively. The goats ate poisonous forbs.

4. Digestion-Reducing Compounds

A. Woody Plants

b. Ether-Extractable Compounds

i. Kudus

There was no significant correlation between the level of ether-extractable compounds in the leaves and the acceptance of woody plants by kudus (Fig 7.25.i.), nor was there any distinguishable difference between preferred and non-preferred species.

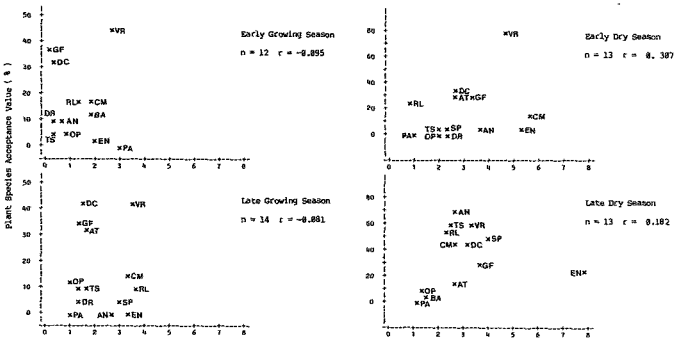


Fig 7.25. The Acceptance of Woody Plant Species in Relation to the Concentration of Ether-extractable Fats and Resins in the Leaves.

1, Kudus

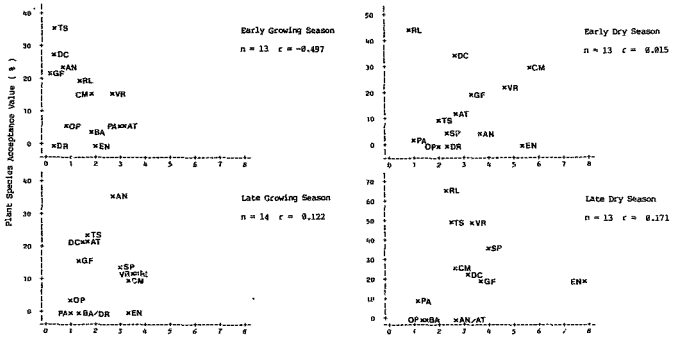


Fig 7.25. The Acceptance of Woody Plant Species in Relation to the Concentration of Ether-extractable Fats and Resins in the Leaves.

ii. Impalas

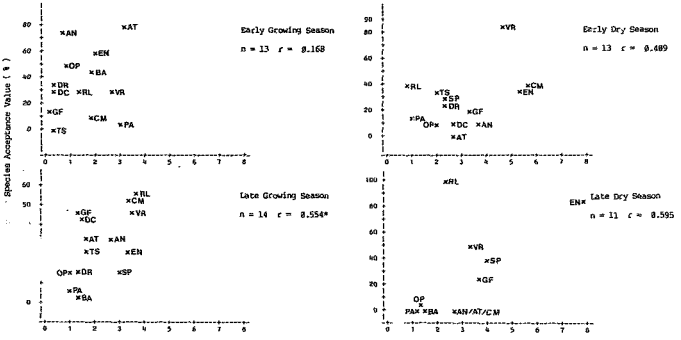


Fig 7.25. The Acceptance of Woody Plant Species in Relation to the Concentration of Ether-extractable Fats and Resins in the Leaves.

iii. Goats

ii. Impalas

Acceptance by the impalas was also not significantly correlated to the concentration of ether-extractable materials in the leaves (Fig 7.25.ii.). The species favoured in the early growing season were of fairly low ether-extract content.

iii. Goats

No significant correlation existed between acceptance by goats and ether-extract content, except for a weak positive correlation in the late growing season, when R. leptodictya and C. molle were favoured (Fig 7.25.iii).

iv. Plant Species Differences

V. rehmannii, C. molle and E. natalensis were comparatively rich in ether-extract. The acceptance value of these plants differed in the growing season but all were of increased acceptance in the dry season. Species low in ether-extractable compounds included four species of low acceptance B. africana, O. pulchra, P. africanum and D. rotundifolia and the favoured plant G. flavescens.

b. Enzyme-inhibiting Polyphenols

i. Kudus

No significant correlation existed between the enzyme-inhibiting polyphenol content of woody plants and their acceptance by kudus (Fig 7.26.i.). The most favoured species in the growing season were of fairly low polyphenol content but there after acceptance appeared to be unrelated to the total polyphenol content.

ii. Impalas

The acceptance of woody plants by impalas was not significantly correlated to the polyphenol content of the leaves except in the late growing season when a high acceptance for A. nilotica, which is rich in enzyme-inhibiting polyphenols, caused a weak positive correlation to develop (Fig 7.26.ii.).

iii. Goats

As for the other animals acceptance of woody plants by goats was not significantly correlated to the concentration of enzyme-inhibiting polyphenols in the leaves (Fig 7.26.iii).

iv. Plant Species Differences

The four species rich in enzyme-inhibiting polyphenols were A. nilotica, C. molle, T. sericea and P. africanum. These species

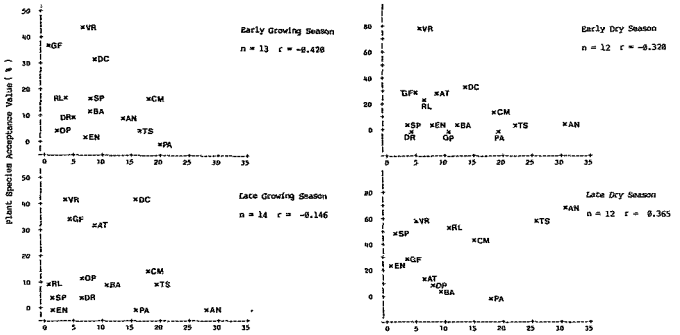


Fig 7.26. The Acceptance of Woody Plant Species in Relation to the Concentration of Enzyme-Inhibiting Polyphenols in the Leaves.

1. Kudus

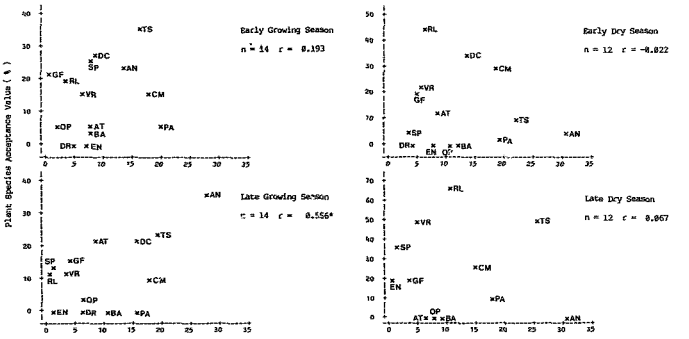


Fig 7.26. The Acceptance of Woody Plant Species in Relation to the Concentration of Enzyme-inhibiting Polyphenols in the Leaves.

ii. Impalas

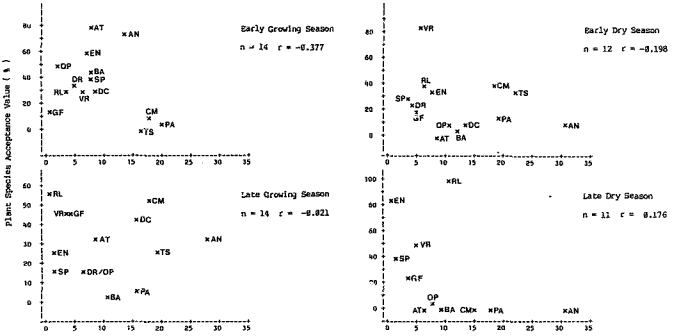


Fig 7.26. The Acceptance of Woody Plant Species in Relation to the Concentration of Enzyme-Inhibiting Polyphenols in the Leaves.

7-56C

iii. Goats

showed a wide range of acceptance values to large ungulates.

c. Condensed Tannins (Proanthocyanidins)

i. Kudus

The overall correlation between the acceptance of woody plants and the condensed tannin content of mature leaves was negative but non-significant. However, there was a clear threshhold effect (Fig 7.27.). Plants containing in excess of 5% dry weight condensed tannin were of low acceptance to the kudus. The preferred plants were not the lowest in condensed tannin concentrations but contained 3 - 3.5% condensed tannin, below the threshhold level.

ii. Impalas

With the exception of T. sericea, which was of moderate acceptance, all plants containing more than 5% condensed tannins were of very low acceptance to impalas. Despite the higher acceptance value of T. sericea, this species made up less than 0.5% of the total diet of the impalas.

iii. Goats

The 5% threshhold level for condensed tannins and plant acceptance was also evident for the goats, though rather less clear cut. As with the impalas, T. sericea was of higher acceptance than the

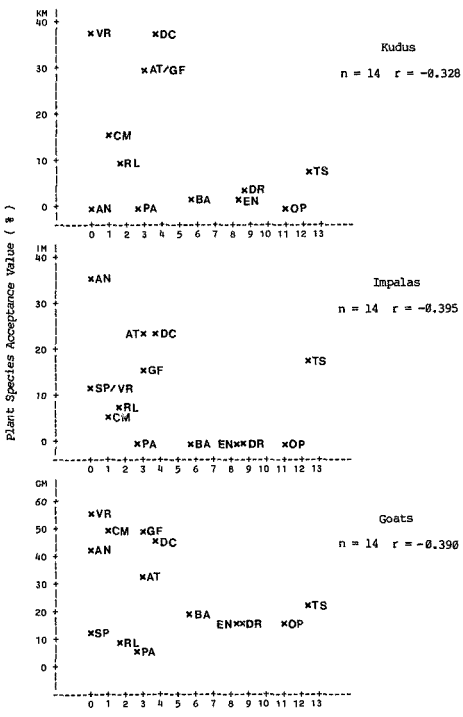


Fig 7.27. The Acceptance of Woody Plant Species in Relation to the Concentration of Condensed Tannin (Proanthocyanidin) in Mature Leaves.

other tannin rich plants, although this may be an effect of small sample size. T. sericea is a very common species but occurs mainly as trees where the leaves are out of reach of the smaller ungulates.

iv. Plant Species Differences

T. sericea, O. pulchra, D. rotundifolia, E. natalensis and B. africana were high in condensed tannin and of low acceptance. Other non-preferred plants are P. africanum and S. pungens, but these do not contain much condensed tannins. P. africanum contains mucilage and saponins while S. pungens is of high fibre content. Of the high condensed tannin plants, B. africana, D. rotundifolia and O. pulchra were eaten when [illegible], presumably before the deposition of condensed tannins, and T. sericea and E. natalensis were eaten in the late dry season when food availability was low. Of the two evergreens S. pungens, which contains no tannins, was preferred over the tannin rich species E. natalensis.

d. Other Digestion-Reducing Compounds

i. Mucilage

The non-preferred plant P. africanum produces a thick mucilaginous slime in solution. This may interfere with the digestibility of this plant.

e. Summary : The Acceptance of Woody Plant Species in Relation to Concentrations of Digestion Reducing Compounds

i. The acceptance of plant species was not correlated to the concentrations of enzyme-inhibiting polyphenols or ether-extractable fats and resins in the leaves.

ii. Condensed tannin (Proanthocyanidin) concentrations acted by a threshhold effect. Plants containing in excess of 5% condensed tannins were of low acceptance to all the animals.

iii. The one woody plant containing a mucilaginous slime was of very low acceptance to all the animals.

B. Forbs

a. Ether-extractable Fats and Resins

i. Kudus

The concentration of ether-extractable compounds in forbs was not significantly correlated to their acceptance by kudus (Fig 7.28.i.). In the growing season the favoured forbs tended to be of rather low ether-extract content, but in the dry season there was no pattern.

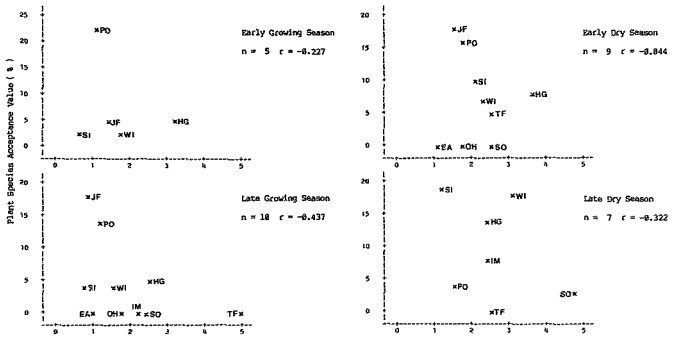


Fig 7.2b. The Acceptance of Forb Species in Relation to the Concentration of Ether-extractable Fats and Resins in Whole Plants.

1. Kudus

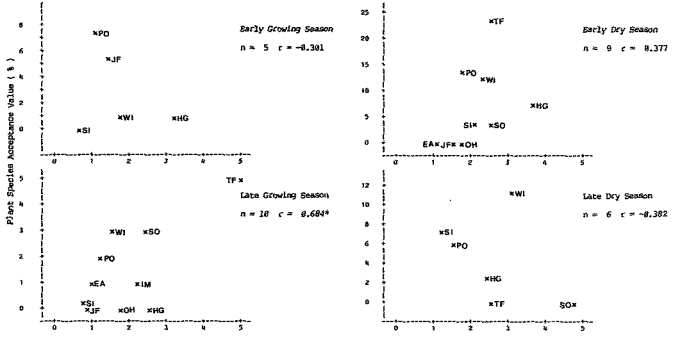


Fig 7.28. The Acceptance of Forb Species in Relation to the Concentration of Ether-extractable Fats And Resins in Whole Plants.

ii. Impalas

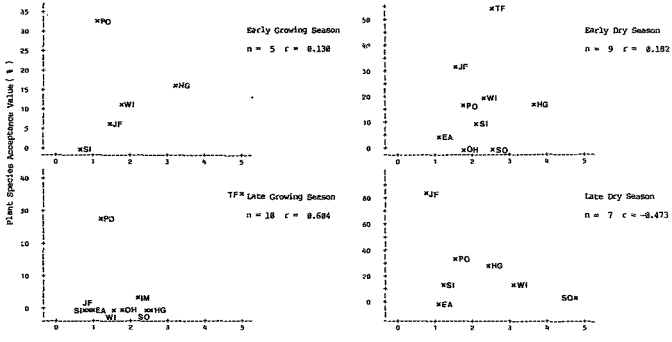


Fig 7.28. The Acceptance of Forb Species in Relation to the Concentration of Ether-extractable Fats and Resins in Whole Plants.

iii. Goats

ii. Impalas

Acceptance was not significantly correlated to ether-extract concentrations (Fig 7.18.ii.). The favoured plants in the early growing season were of low ether-extract content but thereafter plants high in ether-extract were also favoured.

iii. Goats

No significant correlation existed between ether-extract concentrations of forbs and acceptance to goats (Fig 7.28.iii.). The favoured species in the late dry and early growing seasons were relatively low in ether-extractable compounds but species rich in the extract were favoured in the other seasons.

iv. Plant Species Differences

T. forbesii was rich in ether-extract and was favoured by the impalas and goats. Other rich species, S. panduraeforme and H. grisea, were not of such high acceptance. The plants lowest in ether-extract included both favoured species, P. campestris and J. flava, and less preferred plants, E. alsinoides and S. cordifolia.

b. Enzyme-Inhibiting Polyphenols

Compared to woody plants the concentrations of polyphenols in forb

plants were very small. Only W. indica contained appreciable quantities of enzyme-inhibiting polyphenols.

i. Kudus

The concentration of enzyme-inhibiting polyphenols in forbs was not correlated to their acceptance by kudus (Fig 7.29.i.). W. indica was favoured over several species of lower polyphenol content.

ii. Impalas

The relationship between enzyme-inhibiting polyphenols and acceptance of forbs by impalas was similar to that of the kudus, with no significant correlations evident. (Fig 7.29.ii.). The only species high in polyphenols was of intermediate acceptance.

iii. Goats

The species of highest highest polyphenol content was of low acceptance to the goats (Fig 7.29.iii.). The favoured species tended to contain moderate amounts of polyphenol, thus no correlation existed between acceptance to the goats and polyphenol contents of forbs.

iv. Plant Species Differences

Forbs were generally of low polyphenol content. W. indica

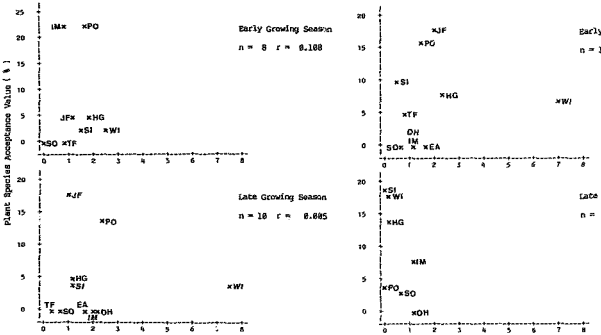


Fig 7.29. The Acceptance of Forb Species in Relation to the Concentration of Enzyme-inhibiting Polyphenols in Whole Plants.

1. Nadus

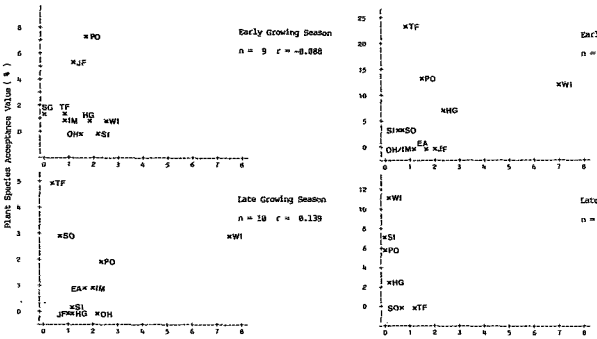


Fig 7.29. The Acceptance of Forb Species in Relation to the Concentration of Enzyme-Inhibiting Polyphenols in Whole Plants.

ii. Impalas

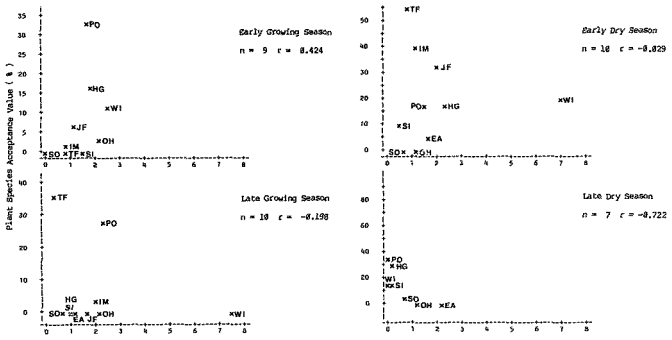


Fig 7.29. The Acceptance of Forb Species in Relation to the Concentration of Enzyme-inhibiting Polyphenols in Whole Plants.

iii. Goats

contained the highest concentration of enzyme-inhibiting polyphenols in the growing season, but concentrations fell to only 0.5% dry weight in the late dry season. It was in this season that W. indica was of highest acceptance to the impalas and kudus.

c. Other Digestion-Reducing Compounds

i. Mucilage

The forb Dicerocarium zanguibarium formed a thick mucilaginous slime in water but was seen to be eaten occasionally by impalas. It was not often encountered by the other animal species.

d. Summary : The Acceptance of Forb Species in Relation to Concentrations of Digestion-Reducing Compounds

i. The concentrations of ether-extractable fats and resins in forbs was similar to that of woody plants, and as for woody plants, acceptance was not related to concentrations of ether-extractable materials.

ii. Concentrations of enzyme-inhibiting polyphenols in forbs were much lower than in woody plants. Only W. indica contained much polyphenol. This species was eaten mainly in the late dry season when the polyphenol content had decreased to very low levels.

iii. The presence of mucilage in plants did not deter the impalas

from feeding on the species.

7.4. DISCUSSION

1. Nutrients

In this study nutrients were not the primary forces governing the selection of browse plants by ungulates. Although correlations between the acceptance of plant species and nutrient contents were generally positive they rarely reached significance.

Correlations with acceptance were only significant in the early growing season for the nutrients nitrogen, phosphorus, and magnesium in woody plants and then only for kudus, which are pure browsers eating little grass.

For forbs any significant correlations were dominated by J. flava, a patchily dispersed forb of extremely high potassium, calcium, magnesium and sodium content.

In the growing and early dry seasons the woody plants favoured by all the animals tended to be of above average nitrogen (protein) and magnesium content. Again this effect was clearest for the kudus. The kudus also tended to favour plants of high potassium content. Selection for phosphorus rich plants was shown only by the kudus in the early growing and early dry seasons. Calcium rich plants were favoured by the kudus and goats in the

late growing season. For impalas this effect was less clearcut. The kudus alone showed a preference for woody species with above average sodium content in the early dry season. In the late dry season, when the availability of browse was low, the acceptance of most plants, including the nutrient poor species, increased and even the weak selection for nutrients observed in the previous seasons ceased to exist. Only magnesium was selected for in the dry season, although this mineral is rarely deficient in the diets of herbivores (A.R.C. 1965). Since magnesium is associated with chlorophyll it may be that the animals were selecting for greenness. Woody plants were not selected for their moisture content.

The relationship between the acceptance of forb species and the nutrient content of whole plants was dominated by J. flava. The impalas favoured this species only in the early growing season when it was rich in potassium, magnesium and water. The kudus had a high acceptance of J. flava in the late growing and early dry seasons when it contained above average concentrations of potassium, calcium, magnesium, sodium and water. The goats showed no preference for this plant until the late dry season when they ate the leafless green stalks.

If J. flava was removed from the regressions there was no significant correlations between the acceptance of forb species and the nutrient concentrations of these plants.

Many studies of dietary selection give conflicting evidence as

to whether or not diet selection by browsers is influenced by nutrient concentrations in the plants.

Studies restricted to the growing season indicate weak selection for nutrients (Lindlof et. al. 1978, Milton 1980, White & Trudell 1980, Leader-Williams et. al. 1981, Vangilder et. al. 1982), while studies in the dormant season find little evidence of nutrient selection (Kuropat & Bryant 1980, Sinclair & Smith 1984).

Year round studies show a pattern of selection similar to that occuring at Nylsvley, whereby weak selection for nutrients is observed in the growing season, but selection is relaxed when food availability is low. Pellew (1982) showed that while giraffe in the Serengeti selected for the young Acacia shoots rich in nitrogen and phosphorus in the growing season, there was no relationship between species selection and nutrients in the dry season.

Similarly kudus in the Kruger National Park select for plants rich in nitrogen and phosphorus and of high moisture content only in the growing season (Novellie 1983). In this season the kudus preferred the nutrient rich leaves of Acacia nigrescens, but in the dry season the utilisation of less nutrient rich broad leaved species increased.

Even in the growing season all nutrient rich plants are not necessarily favoured by the herbivores. At Nylsvley the tree D. rotundifolia had leaves which were rich in all macronutrients. The

leaves were eaten when they were new and soft but once they reached full size they became of very low acceptance to the browsing ungulates. Mature D. rotundifolia leaves have a very gritty texture but leaves of the favoured plants G. flavescens and E. rigida were equally rough in texture. What D. rotundifolia does have, however, is a heavy allocation to digestion-reducing condensed tannins, which seemingly negates the potentially high nutrient gain for animals eating this plant.

The forb S. panduraeforme was very rich in nitrogen, phosphorus, potassium and calcium yet was of low acceptance to the animals. Solanum species frequently possess toxic alkaloids (Watt & Breyer-Brandwijk 1962). S. panduraeforme also gave a strongly positive reaction to alkaloid detection reagents but none of the toxic alkaloids characteristic to the genus have been detected in this particular species.

The Acacia species were of rather lower acceptance, especially to the kudus, than may be expected from their high nutrient content. Possibly the low rate of food intake achieved from these thorny species decreases the overall nutritional value of these plants to the ungulates. The kudus, having the largest body size, would be the most affected by this restriction.

Many plants are rich in both protein and most macronutrients, others may be selected for single factors. D. cinerea leaves were rich in all nutrients when young, but on maturity the levels of all nutrients except nitrogen and magnesium decreased greatly. Yet

the acceptance of this species remained unchanged.

Similarly V. rehmannii, a favoured food plant of the goats and kudus was rich only in magnesium and calcium when mature.

Sodium concentrations in the vegetation at Nylsvley were exceedingly low yet no clear selection for this mineral was observed. Herbivores frequently obtain their sodium requirements from sources other than terrestrial vegetation. Moose obtain their sodium from aquatic vegetation (Belovsky 1981), while caribou migrate to the coast to feed on sodium rich sea-sprayed vegetation (Staaland & Jacobsen 1983). In Wankie National Park, elephants obtained sodium from a salt lick, or when this was removed, from the salty soil remaining at the site. The animals at Nylsvley also had access to a salt lick and probably obtained much of their sodium requirements from this source.

No selection for plants rich in moisture was evident. Although not important at Nylsvley, the moisture content of plants does influence the selection of plant species by desert ungulates (Taylor 1969).

Moran & Hamilton (1980) argued that the maintenance of low protein concentration in the leaves could be a form of plant defence against herbivory. Certainly large herbivores did select against those plants of low nutrient quality but the plant cannot fulfill its own developmental and physiological requirements

without maintaining a pool of nutrients in the leaves (Mooney & Gulman 1982). Also low protein content may merely mean that insect herbivores eat more of the leaves (Fox & Macauley 1977).

The high potassium and low sodium concentrations observed in plants are the reverse of the animals requirements. Plants actively exclude sodium from the roots (Nye & Tinker 1977). It has been suggested that this mechanism is also directed against herbivores (Chapin et. al. 1980), but since the plant has its own physiological needs and nutrient balances, and all plants appear to excrete sodium, it is unlikely that anti-herbivore defence is the primary reason for this phenomenon.

2. Fibre

There was only weak evidence that browsing ungulates select against very fibrous plants at Nylsvley. The impalas and goats avoid fibre by eating leaves rather than shoots. Although kudus eat both leaves and the more fibrous stems, they showed the most clearcut selection against fibre in the leaves of woody plants. In the growing season the kudus had a low acceptance of those plants which contained in excess of 35 ~ 40% NDF, or its constituent ADF, in the leaves. This threshhold effect disappeared in the early dry season, but by the late dry season, a negative correlation had developed between NDF and ADF contents and acceptance by kudus. Impalas did not show this threshhold effect. Discrimination against very fibrous plants was clearest in the dry season and, but for the low acceptance of the A. nilotica, there would have

been a significant negative correlation. The NDF content of woody plant leaves had less effect upon plant species selection by goats. Only in the late growing season were fibrous species of very low acceptance.

On examining the major constituents of total fibre it was found that selection was strongest against ADL. The kudus had a low acceptance for those species of above average ADL content once the leaves achieved full size. For impalas and goats ADL contents only seemed to influence selection in the late growing season.

The potentially digestible fractions of total fibre, namely NDF - ADF and ADF - ADL, had little effect upon the selection of woody plant species.

The selection of forb species by browsing ungulates appeared to be unrelated to the fibre content of whole plants. The stemmy perennial species were eaten increasingly in the dry season, but this is probably a function of availability. The impalas and goats tended to bite off the side leaves or shoot tops of stemmy forbs indicating an avoidance of the fibrous stems. The kudus were less selective in their feeding.

As for nutrients, previous studies on diet selection by herbivores do not all show the same pattern. White-tailed deer in Missouri were found to select against fibre, and especially against lignin (Vangilder et. al. 1982). Studies of small browsers, such as monkeys, indicate avoidance of fibre (Milton

1979, Oates et. al. 1980, Glander 1981), while studies on a variety of northern animals found diet selection to be independent of fibre content (Klein 1976, Bryant & Kuropat 1980).

Fibre may be the main factor in controlling the digestibility of grasses (Van Soest 1982), but for browse the relationship is complicated by the presence of digestion-reducing secondary compounds (Oldemeyer et. al. 1977, Kuropat & Bryant 1980).

3. Digestion-Reducing Compounds

The most abundant digestion-reducing compounds in woody vegetation at Nylsvley were the polyphenols. The two major classes of these phenolics were the enzyme-inhibiting polyphenols and the condensed tannins or proanthocyanidins.

No relationship was found between the acceptance of enzyme-inhibiting polyphenols and plant species acceptance by browsing ungulates, other than a positive correlation in the late growing season for impalas. In this season three of the favoured plants A. nilotica, D. cinerea and C. molle yielded high concentrations of polyphenols.

Correlations between acceptance and condensed tannins in mature leaves were negative but not significant. However there was a definite threshhold effect at 5% dry weight. Plants containing in excess of 5% condensed tannins relative to a Sorghum III tannin standard were of low acceptance. This effect was most clearcut for

the kudus because the impalas and goats had a moderate acceptance for the tannin rich plant T. sericea. This species, however, made up less than 0.5% of the feeding time of these animals

That condensed tannins should influence diet selection by a threshhold effect is consistent with their mode of action. Tannin bound complexes are only stable because sufficient bonds and cross-links are formed (Swain 1979).

Of the five condensed tannin rich species, three were eaten only during the new leaf flush when condensed tannin contents are likely to be low (McKey 1979). Species having a low condensed tannin content, yet being of low acceptance to all three species of browsing ungulate, were the fibrous, armed, evergreen S. pungens and P. africanum which contains a mucilaginous slime and is known to be of very low digestibility to ruminants (van Hoven pers. comm.).

To date the only studies, other than this project, which compare the different effects of condensed tannins and enzyme-inhibiting polyphenols on diet selection by browsers, have been done on leaf eating monkeys. These small animals are not ruminants, although the colobinae do have forestomach fermentation (Waterman et. al. 1988), nor do they digest much cellulose. However, feeding studies indicate that leaf eating monkeys do not discriminate against enzyme-inhibiting polyphenols but avoid plants containing high levels of condensed tannins (Milton 1979, Oates et. al. 1980, Waterman & Wrangham 1981).

Condensed tannins also deter feeding by cattle (Wilkins et. al. 1953), sheep (Harborne 1977), goats (Provenza & Malechek in press), and deer (Cooper-Driver et. al. 1977), all of which are ruminants. Swain (1979) also reports that tortoises avoid plants containing in excess of 2% condensed tannins. Threshhold levels will of course vary slightly depending on the standard used in analysis.

Clearly the two types of tannins have a different effects on diet selection by herbivores. Zucker (1983) hypothesised that condensed tannins, which bind strongly to cellulose as well as to proteins, function to protect plant cell walls against microbial attack by binding to the cell wall cellulose. Ruminants are dependent upon microbial fermentation of cellulose for a significant part of their energy supply. Condensed tannins will render the plant cellulose indigestible, and hence the plant will be a poor source of energy for the ruminant. For non-ruminant herbivores condensed tannins may slow down the turnover rates in the forestomach or caecum, as do digestion-reducing resins (Bryant 1981).

The other class of tannins is the hydrolyzable tannins, included in the measurement of enzyme-inhibiting polyphenols. These tannins bind mainly to proteins and are potentially degradable due to their carbohydrate core (Zucker 1980). That these tannins do not appear to deter feeding by browsing mammals, despite their high astringency, suggests that they are being rendered ineffective due to either the alkaline pH in the rumen, or to degradation by the symbiotic microflora.

A second class of digestion-reducing compounds are the terpenoid and phenolic resins derived from the isoprene pathway rather than from the shikimic acid pathway like tannins. In boreal ecosystems these resins are abundant and are important as deterrents to a wide range of vertebrate herbivores (Bryant & Kuropat 1980, Bryant 1981). Levels of ether-extractable resins in the Nylsvley vegetation were much lower than that found by Bryant (1981) in subarctic habitats, and did not affect the acceptance of plant species by browsing ungulates. In the Karoo sheep exerted a positive selection for ether-extractable materials (Louw et. al. 1967). Ether dissolves out both resins and fatty acids. In temperate and boreal ecosystems resins predominate in the extract (Bryant & Kuropat 1980), especially in the extracts from unpalatable species (Bryant pers. comm), but no detailed analysis has been made of the proportions of the different constituents in ether-extracts from more tropical vegetation.

4. Toxins

No selection against low molecular weight terpenoids was evident in this study. Studies in North America indicate that deer do select against these compounds (Schwartz et. al. 1980a & b). The "essential oils" inhibit digestion by causing a decline in the rumen microfloral population (Oh et. al. 1967, 1968, 1970, Radwan 1972, Nagy et. al. 1964, Schwartz et. al. 1980), but not all essential oils are inhibitory. Monoterpene alcohols cause a greater reduction in microbe nu . than the esters, or

sesquiterpenes (Oh et. al. 1967, Schwartz et. al. 1980).

Saponins are triterpenes. In this study species of woody plants with high levels of foaming activity indicative of saponins were often of low acceptance. Generally saponins have not been reported as having much effect on ruminants, other than being the cause of "bloat" *by certain pasture legumes* (Applebaum & Birk 1979).

The presence of alkaloids in plants did not affect species selection by the browsing ungulates at *Nylsvley. Alkaloids are generally* avoided by grazing animals (Arnold & Dudzinski 1978, Simons & Marten 1971) but not by browsers (Hladick 1977, Oates et. al. 1980, White & Trudell 1980).

Although no specific avoidance of the major groups of toxins was observed it may be that the generalised diet of large herbivores is a technique to avoid the ingestion of deleterious amounts of any one toxin (Westoby 1974).

5. Animal Factors Affecting the Response to Plant Chemistry

i. Browser or Grazer

Kudus are specialist browsers eating little grass. They displayed a much clearer pattern of diet selection in relation to plant chemistry than did either of the mixed grazer-browsers. This may be partly due to sample size as the impalas especially ate very

little browse when green grass was available, or it may be that mixed feeders are not as dependant upon browse for all their food requirements, so are somewhat less selective.

It is also possible that species like impalas may be eating browse in the wet season to supplement only certain nutritional requirements.

ii. Body Size

Although the kudus showed the most clearcut selection against highly fibrous leaves, in fact the smaller animals were probably exerting even stronger selection by selecting against stems. Animals of a small body size require a more concentrated diet, high in nutrients and low in fibre, than do larger animals, due to their higher metabolic rate and small rumen size (Bell 1971, Jarman 1974). Impalas are smaller than kudus but of similar size to goats, yet the goats showed only weak selection against fibre and often ate shoots. The goats were also slightly less selective against digestion-reducing condensed tannins than the other animal species.

iii. Supplementary feeding

Each night the goats received a small supplement of antelope cubes to entice them into their predator-proof overnight shed. This supplementary feeding possibly reduced the selectivity of the goats. Sinclair et. al. (1984) found that supplementary feeding

decreased the selectivity of hares against digestion-reducing compounds, while only the intensity of feeding and not the preference of mule deer was altered by extra rations (Bartman et. al, 1982).

iv. Sensitivity to Toxins : Browser or Grazer

There was little difference in the plant species preference of the kudus and impalas, nor presumably in their ability to cope with plant secondary compounds either through detoxification or avoidance. This suggests that there is little difference between the ability of browsers and mixed-feeders to cope with plant defence chemicals. The ability to detoxify chemicals is probably an effect of experience, as the mixed function oxidase enzymes for detoxification are readily inducible (Brattsen 1979).

v. Detection of Toxins : Alien or Indigenous Animals

Unlike the indigenous animal species the domestic goats failed to avoid poisonous plants including Kalanchoe species, Asclepias species, and the lethally toxic woody geophyte Dichapetalum cymosum. The less poisonous plants were eaten in the growing season but Dichapetalum cymosum was only eaten by the goats in the late dry season when it put out a green flush of new leaves when little other green food was available. These new leaves are defended by monofluoroacetate, a very effective heart poison. A similar situation exists in Western Australia where plants of the genera Gastrolobium and Oxylobium also contain monofluoroacetate.

These plants are not eaten by kangaroos and other indigenous animals but cause severe stock losses to sheep farmers (Arnold & Hill 1972). Thus it appears that alien animals are at a disadvantage in areas where highly poisonous plants exist.

7.5. SUMMARY OF RESULTS

i. Plant species selection is only weakly related to nutrient concentrations in the plants. Selection was strongest for protein and magnesium.

ii. In some plants the advantages of high nutrient concentrations were overridden by the presence of plant secondary compounds.

iii. Selection for nutrients was further relaxed under conditions of low food availability.

iv. Selection against fibre takes the form of selection against stems rather than against fibrous leaves. The fibre components avoided most strongly were NDF and ADF for which there was evidence of a threshhold effect at 35 - 40% dry weight in the growing season. Within these fibre fractions ADL was the component most clearly avoided by the animals.

v. Digestion-reducing condensed tannins exert a clear deterrent effect once the threshhold of 5% dry weight is exceeded. Condensed tannins act by inhibiting microbal degradation of

cellulose and thus limit the supply of energy to ruminants via microbial fermentation of cellulose in the rumen.

vi Enzyme-inhibiting polyphenols do not deter feeding by browsing ungulates, neither do ether-extractable resins at the amounts found in savanna vegetation.

vii. The presence of toxic plant secondary compounds did not deter the animals from feeding, but may be responsible for the generalised diet of large herbivores.

viii. Plant species selection in relation to plant chemistry was more clearcut for the kudus, as pure browsers, than for the impalas and goats which also eat grass.

ix. There was no difference in the ability of indigenous browsers (kudus) and preferential grazers (impalas) to cope with plant toxins.

x. The alien goats failed to avoid the few highly poisonous plant species which were never seen to be eaten by the indigenous impalas and kudus.

CHAPTER 8.

FINAL DISCUSSION

8.1. The Chemical and Structural Basis of Food Selection by Browsing Ungulates

A. Nutrients

In models of optimal foraging behaviour protein and digestible energy are usually considered to be the nutrients most likely to be limiting to the animals (Pyke et. al. 1977). Large herbivores are constrained by the rate at which they can process the large bulk of low quality food necessary for an adequate intake of nutrients (Westoby 1974).

Owen-Smith & Novellie (1982), in their clever-ungulate model, defined a large generalist herbivore as a short-term maximiser for nutrient intake. Protein was assumed to be the target nutrient as it is generally assumed that African ungulates are protein-limited (Bell 1971, Sinclair 1975). However, the outcome of the model indicated that digestible energy was more likely to be limiting.

i. *Woody Plants*

At Nylsvley nitrogen (protein) concentrations in woody plant leaves were significantly correlated with acceptance to kudus in

the early growing season. In the late growing season and early dry season the plant species favoured by the kudus were of significantly higher protein concentration than the non-preferred group of plant species. In the late dry season, when the favoured deciduous browse plants had shed most of their leaves, the kudus ate more of the low protein, evergreen species. For impalas and goats leaves of the favoured woody plant species were only of significantly greater protein concentration than those of non-preferred plants in the late growing season.

The concentration of all macronutrients were covariant in the leaves but the correlation of plant species acceptance by browsing ungulates was stronger with protein than with the associated nutrients.

Belovsky (1978) suggested that herbivores may select different plants to meet different requirements i.e. one plant may be selected to meet protein requirements and another to meet mineral or energy requirements. This idea was not supported by this study as the variation in the proportions of different nutrients within the plants was not great.

ii. Forbs

As for woody plants the nutrient concentrations in forbs covaried. The acceptance of forb species by browsing ungulates was not significantly correlated to the concentration of protein or minerals in whole forbs. The concentration of nutrients in forbs

was generally somewhat higher than that of woody plants.

B. Fibre

The rate of digestion of plant fibre influences the turnover time of the rumen contents, and ultimately the ingestion rate of food (Van Soest 1982). The fermentation of plant cell walls is a comparatively slow process. If an animal is to maximise its intake of nutrients from a fixed bulk of food it should select plants of low fibre content. Evidence for such selection at the *species* level is equivocal. Leaf-eating primates generally select leaves of low fibre content (Milton 1979, Oates et. al. 1980, Glander 1981), but boreal herbivores show little selection against fibrous plants (Klein 1978, Kuropat and Bryant 1980).

i. Woody Plants

In this study, for the kudus at least, there was evidence of a threshhold effect in the growing season, whereby plants containing in excess of 35 - 40% NDF or ADF in the leaves tended to be of low acceptance. In the dry season the goats showed no selection for plant species low in fibre, but the species favoured by the kudus and impalas were of significantly lower NDF content than that of the *non-preferred* plants. Of the major components of cell wall fibre ADL was the most clearly negatively related to plant species acceptance.

In general smaller animals have a higher metabolic rate than

larger animals and are less tolerant of fibre in the diet (Bell 1971). Yet the impalas and goats appeared to show weaker selection against fibre than did the larger-bodied kudus. Selection against fibre possibly operates most strongly at the level of plant-part selection rather than species selection. On the whole the variation in the fibre content is less between the leaves of *different species* than it is between leaves and stems of the same species. In all the woody plant species analysed the hardened stems were more fibrous, and usually more *lignified* than the leaves. The kudus ate mainly shoots, including stems, but the impalas selected leaves and ate very little stem material. The goats fed on both single leaves and shoots. By their selection of leaves the two smaller animal species avoided the ingestion of the *most fibrous* plant material.

For some plants such as O. pulchra and B. africana the deposition of fibre in the leaves is initially very rapid. Leaves of these species tended to be eaten only in the immature phase while still of low fibre content. Thus phenological selection may also be due to the avoidance of fibre.

ii. Forbs

Many of the favoured forb species were of high fibre content. Yet as for woody plants the impalas, and to a lesser extent the goats, tended to bite the leaves off the stems whenever the growth form of the plant allowed, thus avoiding the ingestion of fibrous stem tissue.

C. Ratio of Metabolic Constituents to Structural Carbohydrates

Plant tissues consist of structural carbohydrates which form the cell walls and cytoplasmic contents including proteins and soluble carbohydrates. Bell (1971) suggested that the ratio of the metabolic constituents (m) to structural carbohydrates (c) was a useful indication of vegetation quality as food for herbivores.

i. Woody Plants

In this study the m/c ratio was not significantly correlated to the acceptance of woody plant species by ungulates. (Late growing season $n = 13$, kudus $r = 0.176$, impalas $r = 0.435$, goats $r = 0.222$). Dicotyledonous plants, unlike the grasses studied by Bell (1971), contain not only metabolites and structural carbohydrates but also plant secondary compounds, which in the case of tannins may comprise a large proportion of the dry weight of the plant. Tannins are associated both with the cytoplasm (hydrolyzable tannins) and with the cell walls (condensed tannins),(Zucker 1983).

ii. Forbs

The forb species did not contain high levels of tannins but do contain other secondary chemicals, particularly toxins. As for the woody plants the acceptance of forbs by browsing ungulates was not correlated to the m/c ratio (Late growing season $n = 10$, Kudus $r =$

0.577, impalas r = -0.177, goats r = -0.239).

D. Digestion-Reducing Compounds

a. Tannins

i. Woody Plants

In this study plants with leaves containing more than 5% dry weight of condensed tannins (proanthocyanidins), relative to a Sorghum III tannin standard, were generally of low acceptance. Total polyphenols on the other hand appeared to have little effect upon plant species selection.

Condensed tannins generally seem to have a greater deterrent effect upon mammalian herbivores than hydrolyzable tannins (included in total polyphenols). This has been attributed to the stronger in vitro protein-binding ability of condensed tannins (McLeod 1970, Waterman 1988).

In this study polyphenols were not measured by the more usual Folin-Denis procedure but by the Jerumanis method (Jerumanis 1972), a technique used by brewers as it correlates more strongly with the enzyme-inhibition properties of polyphenols than most other techniques (Daiber 1975).

Plants other than T. sericea which contained high concentrations of condensed tannins had fairly low levels of

enzyme-inhibition activity. This suggests that within the plants condensed tannins do not have a strong protein binding capacity.

Zucker (1983) proposed that hydrolysable tannins function to inactivate digestive enzymes, but condensed tannins bind with the cellulose of cell walls, thereby protecting the cells against microbial attack. Ruminants are dependent upon the microbial degradation of cellulose for much of their energy requirements (Van Soest 1982). Thus the presence of high levels of condensed tannins in the plant tissues may restrict the microbial fermentation of cellulose in the rumen, and so limit the amount of energy that the herbivore can obtain from the plant tissues.

ii. Forbs

Forbs generally contained low concentrations of polyphenols relative to the amount found in woody plants. The acceptance of forb species by ungulates was not related to the concentrations of enzyme-inhibiting polyphenols in whole plants.

b. Ether-Extractable Compounds

Ether-extractable resins have been found to be very important deterrents to vertebrate herbivores in boreal plants (Bryant & Kuropat 1980, Bryant 1981).

i. Woody Plants

The quantity of ether-extractable compounds in savanna plants was far less than that recorded from boreal plants, and appeared to have no effect upon plant species selection by browsing ungulates.

ii. Forbs

Quantities of ether-extractable compounds present in forbs were similar to those in woody plants, but had no discernable effect upon plant species selection by kudus, impalas or goats.

E. Toxins

Browse plants contain a diverse array of secondary compounds some of which are potentially toxic to ungulates. These substances may either interfere with the metabolic processes of the herbivore, or affect digestive processes by their action upon the rumen microflora.

Many potentially toxic substances are degraded by the mixed function oxidase systems common to most forms of life (Schuster 1964, Brattsen 1979). Ruminants and animals with a symbiotic microbial population in the foregut are thought to gain additional protection by detoxification of many compounds by the microflora (Foose 1982).

The mixed function oxidase system can only cope with small quantities of a variety of toxins. Thus Freeland and Janzen (1974) proposed that herbivores should select their diet in order to minimise the ingestion of large quantities of any one toxin.

i. Woody Plants

The herbivores at Nylsvley ate a wide variety of woody plant species but little selection against plants containing terpenoids, or alkaloids was detected. Only those plants exhibiting a high degree of foaming activity in solution, indicative of saponins, were often of low acceptance to kudus, impalas and goats. The only woody species known to be avoided due to the presence of toxins in the leaves was the poisonous woody geophyte Dicapetalum cymosum. This plant contains a lethal toxin monofluoroacetate and was never seen to be eaten by the kudus and impalas.

ii. Forbs

Alkaloids appeared to be more abundant in forbs than in woody plants. Saponins and terpenoids were also common. No avoidance of plants containing alkaloids was evident except for a few species containing specific potent forms, for example the Kalanchoe species which contain a neuromuscular toxin "cotyledontoxin." Similarly the impalas and kudus were not seen to eat Nidorella resedifolia which also contains a potent alkaloid. The Asclepias species containing cardiac glycosides were also not eaten. No selection against plants containing terpenes or saponins was

evident.

Thus herbivores appear to be deterred from feeding only by a few highly potent toxins. This partially agrees with Freeland and Janzen's (1974) hypothesis that large herbivores should select foods of low secondary compound content.

Freeland and Janzen (1974) also proposed that the generalised diet of large herbivores was a mechanism for avoiding the ingestion of too much of any one compound. This study agrees with this theory better than the idea of Westoby (1978) that large herbivores eat a wide variety of plant species in order to obtain a balanced intake of nutrients, as the relative concentrations of nutrients in the plants at Nylsvley were fairly similar in most species. Also the rumen microflora synthesise amino-acids and vitamins B and K (Van Soest 1982), so freeing the ruminant from the need to find an external source of these compounds.

F. Effects of Plant Structural Defences

It is hard to visualise large thorns and spines on plants as being defensive against any other class of herbivores except the vertebrates. Brown (1960) proposed that these structures deter browsing by herbivorous mammals to some extent but should not be expected to provide absolute protection to the plant as animals may have counter-adapted to their presence.

i. Woody Plants

The thorns of the Acacia species and spines of Dichrostachys cinerea restrict the bite size of the animals to single leaves or small leaf clusters between the thorns or spines. The rate of food intake achieved by the kudus when feeding on these armed species was no greater than that of the impalas and goats, being less than 1 g/min from A. nilotica and A. tortilis and approximately 2 g/min from the larger leaved D. cinerea. Yet when feeding upon unarmed species the intake rate of the kudus averaged 7.5 ± 3.1 g/min, more than double that of the impalas and goats. Thus it would appear that the presence of thorns or spines have a greater effect upon the rate of food intake achieved by the kudus than by the impalas and goats.

The impalas favoured the Acacia species and D. cinerea. They are narrow muzzled animals normally eating single leaves at a rapid biting rate even from unarmed species. The intake rate of the goats is similar to that of the impalas but goats eat more shoots and have slower biting rate. Experimental removal of thorns showed that while the presence of thorns restricted the intake rate from the small leaved Acacias, the spines of D. cinerea had little effect on the intake rate of goats due to the larger leaves of this species. Goats favoured D. cinerea but had a slightly lower acceptance of the Acacia species. The kudus also had a high acceptance of D. cinerea even though their rate of intake from this species was significantly less than that from unarmed plant species. The Acacias were of slightly lower acceptance to kudus

than was *D. cinerea*.

These thorny and spiny plants are probably favoured, despite the restricted bite size, because they are rich in protein and low in fibre and condensed tannins, therefore offering a concentrated source of nutrients. The actual rate of intake of nutrients is greater from the unarmed, large leaved species, but for a given quantity of nutrient injested the amount of diluting fibre and secondary compounds is proportionally much greater.

The evergreen species *S. pungens* bears structural deterrents in the form of sharp spines at the tip of each leaf. *S. pungens* was a favoured dry season food plant, especially for the kudus which bit off large shoots despite the stiff spiky leaves. The impalas also were relatively unaffected by the spines as they bit off single leaves in rapid succession. The goats appeared to be more deterred by the leaf spines. They seemed to find difficulty in pulling off single leaves with their prehensile lips. They ate mainly small shoots at a slow rate and achieved a poor intake rate. The impalas and kudus favoured *S. pungens* over the unarmed evergreen *E. natalensis* despite the sharp spines. *S. pungens* has a slightly higher nitrogen content than *E. natalensis* and is equally fibrous. The main difference in the chemistry of these two evergreens is that *E. natalensis* is rich in condensed tannins while the armed species is free of these deterrent compounds. The goats, however, favoured *E. natalensis* over *S. pungens*. This behaviour was probably due to the scarcity of the latter species in their home range and the low intake rate they achieved when

feeding on this species.

ii. Forbs

Few forb species had thorns or spines. The Solanum species had small, hooked stem spines possibly more effective against crawling insects than large herbivores which bit off the relatively large leaves without becoming caught by the thorns. The Asparagus species had leaves and sharp hooked thorns. These did appear to deter herbivores. The impalas and goats nibbled at the filamentous leaves, but the kudus only eat the soft, new shoots before the thorns had hardened.

Thus it seems that as proposed by Brown (1960) structural deterrents are not an absolute defence against browsing by large herbivores. However, they do offer a measure of protection to the plant by restricting the rate of loss of leaf tissue to large herbivores.

G. The Effect of Abundance on Plant Species Selection

The staple plant species in the diet of a herbivore are not necessarily the most preferred plants (Petrides 1975). Often animals favour rare plants rather than the most abundant species (Martin 1974, McKey et. al. 1980, Oates et. al. 1980, Glander 1981, Pellew 1982).

i. Woody Plants

The acceptance of woody plants by browsing ungulates at Nylsvley was not correlated to the abundance of available browse material. Neither were the rare species favoured when ever they were encountered. Rare species, like the common species, showed a variety of acceptance values to browsing ungulates.

The dominant woody plants of the Burkea Savanna, B. africana, O. pulchra and T. sericea (Rutherford 1982) were not favoured by browsing ungulates, but in the Acacia savanna the dominant trees were generally of high acceptance to browsers. The staple dietary species D. cinerea and G. flavescens were both locally abundant and of high acceptance value. Neither these species or the Acacia species were of high condensed tannin content, and all were rich in protein. The dominant plants of the Burkea savanna were, in contrast, high in condensed tannins and low in nutrients.

ii. Forbs

No data was available on the abundance of forbs over the study period. The abundance of individual species of forbs was markedly different in the two years of the study. Forbs other than the few high poisonous species are probably eaten in relation to their abundance as found for caribou in Alaska (Trudell and White 1981).

H. A Multivariate Approach to Plant Species Selection

Browse plants fall into groups of distinct patterns of acceptance to browsers. The favoured plants are those such as G. flavescens which are of high acceptance to the animals at all times. Included in this group are species like C. molle which are of somewhat lower acceptance but are the first to be of increased acceptance as the availability of the favoured species declines in the early dry season. On the other side are the non-preferred species. These include plants of low acceptance to browsers for most of the year. Some like P. africanum may never be eaten in quantity, while others, such as E. natalensis are eaten only in the late dry season when the availability of browse is very low.

No single plant factor can be used to predict which plant species will be eaten by browsing ungulates and which will not. Generally plants rich in protein were favoured, with the exception of D. rotundifolia which also contains high levels of condensed tannins. Plant species of high condensed tannin content were of low acceptance to browsing ungulates, but so were several other species containing little tannins. Plant species selection possibly involves a trade off between 'good' and 'bad' plant factors. Multivariate analysis was used to determine whether plant species selection was governed by a composite set of plant factors (see appendix 9 for methods).

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i. Selection of Woody Plants

a. Discriminant Function Analysis

The woody plant species were classified into a priori groups. 'Preferred' plants were those of high acceptance or of moderate acceptance but eaten increasingly in the early dry season. 'Non-preferred' plants were those of consistently low acceptance to the browsing ungulates and species eaten only in the late dry season when food availability was at a minimum.

Firstly a stepwise discriminant analysis of the chemical measures was run to identify the most significant variables in mature leaves of woody plants. These were nitrogen, calcium, potassium, ADL, NDF - ADF and condensed tannin (Table 8.1.), with condensed tannin being the single most significant variable.

The chemistry of the mature green leaves of the plants in these two preference groups was then compared by discriminant function analysis which identifies the linear combination of chemical measures that best differentiates between the two groups of plants.

A two factor discriminant function model based on protein and condensed tannin explained 59% of the variation between 'preferred' and 'non-preferred' plant species (Table 8.2.). S.pungens was classified along with the preferred group by this

Table 8.1, Stepwise Discriminant Analysis of the Chemical Content of Mature Leaves of Woody Plants

Nutrients	Significance Prob>F		Canonical r2
Protein	0.03	*	0.33
Calcium	0.04	*	0.30
Potassium	0.08	*	0.24
Sodium	0.19		0.14
Magnesium	0.28		0.10
Water	0.53		0.03
Phosphorus	0.62		0.02
Non-Nutrients			
Condensed Tannin	0.006	*	0.51
Neutral Detergent Fibre minus Acid Detergent Fibre	0.07	*	0.27
Acid Detergent Lignin	0.07	*	0.26
Ether-extract	0.20		0.14
Enzyme-inhibiting Polyphenols	0.46		0.05
Acid Detergent Fibre minus Acid Detergent Lignin	0.61		0.02

* Significant

Table 8.2. *Discriminant Function Analyses of Preferred and Non-preferred Woody Plant Species*

	Chemical Variables	Canonical r2	ProbF	Misclassified Species
1.	Nitrogen and Condensed Tannin	0.59	0.008	Strychnos pungens
2.	Nitrogen and Enzyme-inhibiting Polyphenols	0.34	0.098	Burkea africana Rhus leptodictya Vitex rehmannii
3.	Nitrogen, Condensed Tannin and Neutral Detergent Fibre	0.66	0.018	None
4.	Nitrogen, Condensed Tannin and Acid Detergent Fibre	0.60	0.022	None
5.	Nitrogen, Condensed Tannin and Acid Detergent Fibre minus Ash	0.59	0.025	Strychnos pungens
6.	Nitrogen, Condensed Tannin and Acid Acid Detergent Lignin	0.59	0.026	Strychnos pungens
7.	Nitrogen and Neutral Detergent Fibre	0.53	0.024	Burkea africana Combretum molle Dombeya rotundifolia
8.	Nitrogen and Acid Detergent Fibre	0.46	0.035	Combretum molle Dombeya rotundifolia Vitex rehmannii
9.	Nitrogen and Acid Detergent Fibre minus Ash	0.39	0.054	Combretum molle Dombeya rotundifolia Vitex rehmannii
10.	Nitrogen and Acid Detergent Lignin	0.33	0.011	Burkea africana Vitex rehmannii
11.	Calcium and Condensed Tannin	0.57	0.010	Dichrostachye cinerea Peltophorum africanum Strychnos pungens

model (Fig. 8.1.). It is an evergreen of high fibre content but contains no condensed tannins. A discriminant models including the major fibre fractions NDF or ADF classified S. pungens more correctly but otherwise was little improvement upon the model of protein and condensed tannin only (Fig 8.2.). Although S. pungens was of low acceptance in the late growing season it was of similar acceptance to C. molle for the rest of the year. Thus is really intermediate between the 'preferred' and 'non-preferred' groups.

Discriminant function models using only protein and fibre measures, or condensed tannins with nutrients other than protein, were less successful in classifying the plants according to their acceptance by browsing ungulates (Table 8.2.). Plots of the actual late growing season acceptance values for woody plant species against the canonical coefficients showed that plants fell into distinct groups (Fig 8.1.). On the high protein, low condensed tannins side the preferred group of species divided into those of high acceptance whenever they were available, and those species of low to intermediate acceptance in the growing season but being the first of the dry season reserve species to be of increased acceptance when the availability of the more favoured species declines. The latter group consisted of the two evergreen species with low condensed tannin contents, and C. molle which although low in condensed tannins is of rather low protein content. The acceptance of Acacia species varied, for impalas Acacias were of high acceptance, the goats had a rather lower acceptance of these plants possibly due to the restrictive effect of the thorns on food intake by goats. A low encounter rate with

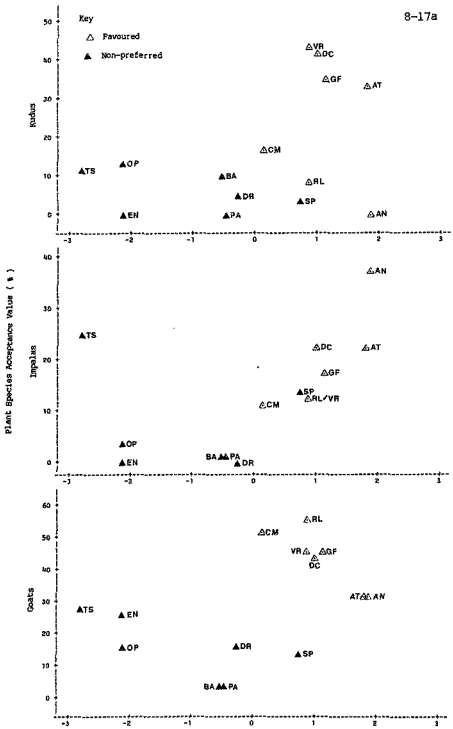

Fig 8.1. Discriminant Function Analysis : The Acceptance of Woody Plant Species in Relation to the Canonical Values with Mature Leaf Nitrogen and Condensed Tannin (Proanthocyanidin) Concentrations as the Variables.

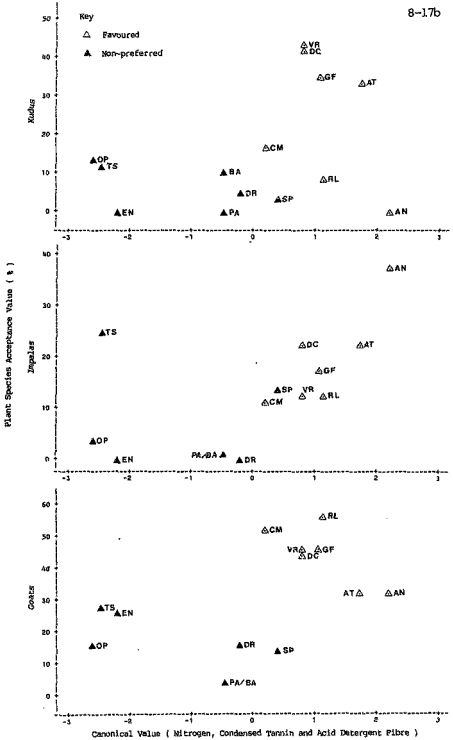

Fig 8.2. Discriminant Function Analysis : The Acceptance of Woody Plant Species in Relation to the Canonical Values with Mature Leaf Nitrogen, Condensed Tannin (Proanthocyanidin) And Acid Detergent Fibre Concentrations as the Variables.

Acacia trees confounded the picture for kudus. A. nilotica was of low acceptance in this study, but favoured in the following year (Cooper & Owen-Smith 1984). Non-preferred species also divided into two groups; the high condensed tannin, low protein group and a second group consisting of two species of intermediate condensed tannin content with low protein contents plus one plant of high protein and high condensed tannin content.

The intake rate achieved from plant species influences the rate of ingestion of nutrients and non-nutritive compounds. Discriminant function models using rate of ingestion of compounds rather than leaf concentrations were only a slight improvement upon previous models (Table 8.3.). For the protein and condensed tannin model the separation between preferred and non-preferred plants was slightly clearer when using rates of intake rather than leaf concentrations (Fig 8.3.). A more significant increase in variance explained was in the model based on the intake rate of protein, condensed tannin and ADF, but the separation between preferred and non-preferred plants was little clearer than that achieved by the model excluding ADF. Thus it appears that the animals distinguish between good food plants and non-preferred plants on the basis of simultaneous rates of ingestion of condensed tannins, protein and to a lesser extent fibre.

Discriminant function analysis requires that the variables, in this case chemical components, be independent of one another. Concentrations of nitrogen and condensed tannins were not

Table 8.3. Discriminant Function Analyses of Preferred and Non-preferred Woody Plant Species based on rates of intake of Chemical Compounds by *Browsing Ungulates*.

Chemical Variables (Rate of Intake)	Canonical r2	ProbF	*Misclassified Species*
i. Kudus			
Nitrogen and Condensed Tannin Intake	0.59	0.008	Strychnos pungens
ii. Impalas			
Nitrogen and Condensed Tannin Intake	0.62	0.005	Strychnos pungens
iii. Goats			
Nitrogen and Condensed Tannin Intake	0.59	0.008	Strychnos pungens
i. Kudus			
Nitrogen, Condensed Tannin and Acid Detergent Fibre Intake	0.72	0.004	Strychnos pungens
ii. Impalas			
Nitrogen, Condensed Tannin and Acid Detergent Fibre Intake	0.66	0.011	*Strychnos pungens*
iii. Goats			
Nitrogen, Condensed Tannin and Acid Detergent Fibre Intake	0.63	0.017	Strychnos pungens

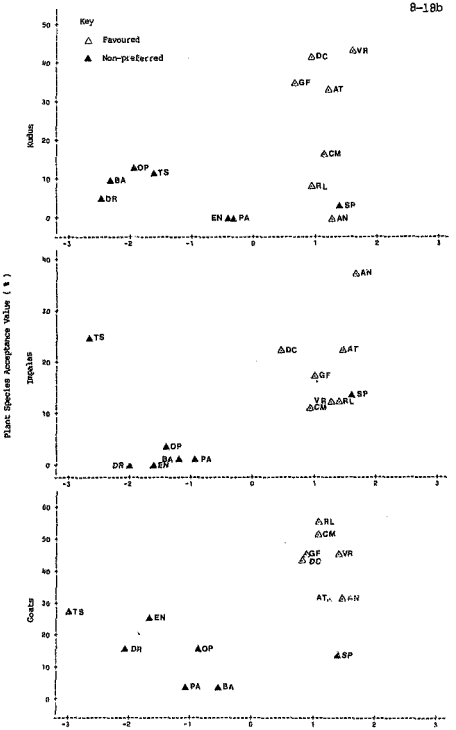

Fig 8.3. Discriminant Function Analysis : The Acceptance of Woody Plant Species in Relation to the Canonical Values with Rate of Intake of Nitrogen and Condensed Tannin (Proanthocyanidin) from Mature Leaves as the Variables.

intercorrelated (Fig 8.4.), but the relationship between NDF and condensed tannins was strong (Fig 8.5.). It has been suggested that *condensed tannins are* associated with hemicellulose, but the correlation with ADF was only slightly weaker than that with NDF (n = 14, r = 0.563*, excluding S. pungens r = 0.659*). Thus in the discriminant model the inclusion of fibre is possibly exaggerating the effect of the condensed tannins. That condensed tannins are associated with cell wall fibre is further supported by the fact that concentrations of the other category of tannins, which have mainly an enzyme-inhibitory action, are not correlated to NDF contents.

b. Principal Components Analysis

Principal components analysis was used to determine the main source of between species variability in chemical factors in mature leaves of woody plants, with no a priori classification being imposed on the data.

The first axis of the principal components analysis accounted for 34% of the between species variation. Factor loadings were strongly negative for ADL, ADF - ADL and condensed tannins and strongly positive for protein and minerals all of which are covariant. Enzyme inhibiting po[illegible]'s and ether-extractable compounds were of little [illegible]n the first axis but dominated the second axis (Table [illegible]

Thus principal component analysis indicated that the major

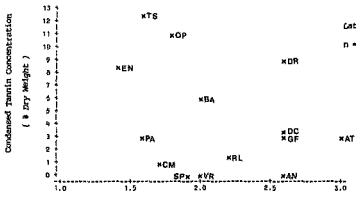

Fig 8.4. The Relation Between Condensed Tannin (*Proanthocyanidin*) and Nitrogen Concentrations in the Mature Leaves of Woody Plant Species

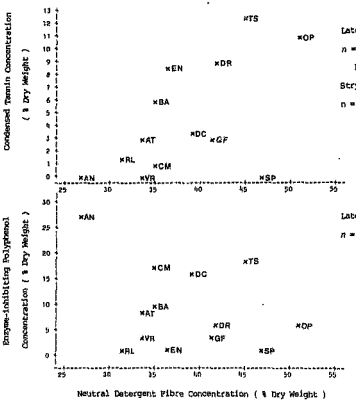

Fig 8.5. The Relation Between Phenolic Constituents and Neutral Detergent Fibre Concentrations in the Mature Leaves of Woody Plant Species

difference between woody plant species lies in the proportions of cell wall to cell contents. A plot of the factor scores for each plant reveals that plants divide roughly into two groups on the basis of the first axis i.e. ADF and condensed tannin to nutrients, but not on the basis of the second axis (Fig 8.6.). These groupings are similar to the preferred and non-preferred groups of plants used in the discriminant function analysis.

Plants differ mainly in their concentrations of ADF, especially the ADL fraction, and condensed tannins in relation to the concentrations of nutrients, particularly cations. Animals select plants on a similar basis but are more sensitive to condensed tannins than ADL and to protein rather than cations, therefore there was no correlation between acceptance values and factor scores (Kudus $r = 0.073$, impalas $r = 0.263$, goats $r = 0.419$).

The major component of ADF affecting food selection by browsing ungulates was ADL. Both condensed tannin and lignin are polyphenols derived from the shikimic acid pathway (Haslam 1974) and both act to restrict the degradation of cell wall cellulose by microbes (Swain 1979, Zucker 1983). Ruminants are largely dependent upon the microbial digestion of cellulose for their energy requirements (Van Soest 1982). Thus the presence of high concentrations of condensed tannin and lignin may restrict the energy supply the ruminant can obtain from the plant tissues as both act to limit cell wall digestion.

Table 8.4. Principal Components Analysis of the Chemical Components of Mature Leaves of Woody Plants

Chemical Components	First Axis	Second Axis
% Variance	34	17
Acid Detergent Lignin	-0.62 *	0.51
Condensed Tannin	-0.49	0.64
Acid Detergent Fibre minus Acid Detergent Lignin	-0.39	-0.24
Enzyme-inhibiting Polyphenols	-0.17	-0.29 *
Neutral Detergent Fibre minus Acid Detergent Fibre	-0.01	-0.75 *
Ether-extract	-0.23	-0.68
Protein	0.64	-0.07
Magnesium	0.66	0.30
Sodium	0.67	-0.02
Phosphorus	0.67	0.45
Water	0.68	0.27
Calcium	0.77	-0.07
Potassium	0.88 *	0.10

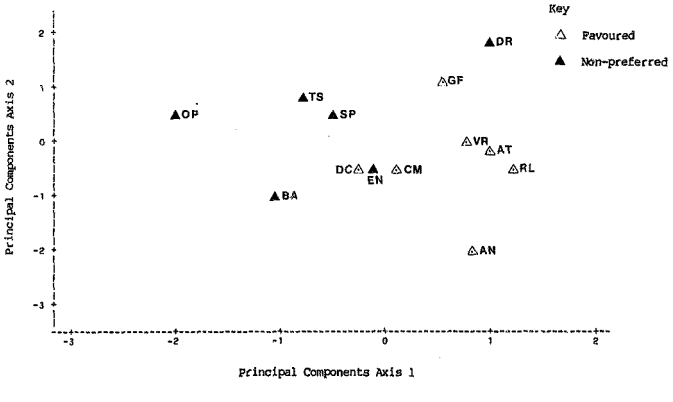

Fig 8.6. Principal Component Analysis of Woody Plant Species According to the Concentrations of Chemical Components in the Mature Leaves.

ii. Forbs

a. Discriminant Function Analysis

Forb species, other than a few highly poisonous plants, cannot be clearly classified into preferred and non-preferred groups. This is due to the effects of small size, patchy distribution and differences in abundance between the two years over which this study was run. The 10 common forbs were tentatively placed into two preference groups, preferred plants being those of high acceptance to at least one of the animal species during the growing season. However, stepwise discriminant analysis did not identify any chemical factors significantly different in concentration between the two groups of forbs (Table 8.5). Similarly no significant discriminant function model could be found (Table 8.6.). This suggests there was no real chemical difference between forbs which are of high acceptance to some browsing ungulate species in the growing season and those which were not favoured.

b. Principal Components Analysis

The first axis in principal components analysis accounted for 47% of the variation between forb species.The plants were separated out by cell wall components, especially ADL, versus nutrients (Table 8.7.). This division is very similar to the first axis of the principal components analysis of woody plants.

Table 8.5. *Stepwise Discriminant Analysis of the Chemical Content of Whole Forbs*

Nutrients	Significance Prob>F	Canonical r2
Phosphorus	0.21	0.19
Magnesium	0.22	0.18
Calcium	0.41	0.09
Potassium	0.48	0.06
Water	0.61	0.03
Sodium	0.63	0.03
Protein	0.91	0.00
Non-Nutrients		
Ether-extract	0.34	0.11
Acid Detergent Fibre minus Acid Detergent Lignin	0.38	0.10
Enzyme-inhibiting Polyphenols	0.49	0.06
Acid Detergent Lignin	0.70	0.02
Neutral Detergent Fibre minus Acid Detergent Fibre	0.99	0.00

* Significant at 95%

Table 8.6. Discriminant Function Analyses of Preferred and Non-preferred Forb Species

Chemical Variables	Canonical r2	Prob>F	Misclassified Species
Nitrogen and Acid Detergent Fibre	0.14	0.583	Evolvulus alsinoides, Hermannia grisea Solanum panduraeforme, Tephrosia forbesii
Phosphorus and Acid Detergent Fibre	0.40	0.102	Evolvulus alsinoides, Indigofera macra
Phosphorus, Acid Detergent Fibre and Ether-extractable Compounds	0.48	0.240	Evolvulus alsinoides

Table 8.7. Principal Components Analysis of the Chemical Components of Whole Forbs

Chemical Components	First Axis	Second Axis
% Variance	47	17
Acid Detergent Lignin	-0.92 *	-0.19
Ether-extract	-0.50	-0.35
Neutral Detergent Fibre minus Acid Detergent Fibre	-0.41	-0.13
Acid Detergent Fibre minus Acid Detergent Lignin	-0.32	0.69
Enzyme-inhibiting Polyphenols	-0.27	0.81 *
Phosphorus	-0.33	-0.54 *
Water	0.64	0.05
Protein	0.68	-0.50
Potassium	0.85	0.00
Sodium	0.88	0.26
Magnesium	0.92	0.22
Calcium	0.94 *	0.07

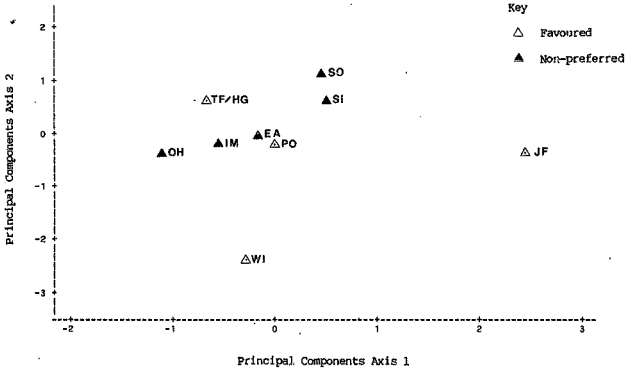

Fig 8.7. Principal Component Analysis of Forb Species According to the Concentrations of Chemical Components in the Flowering Plants.

Regression of factor scores against plant species acceptance showed that for impalas and goats acceptance was not correlated to proportions of cell wall and nutrients in whole forbs (impalas $r = -0.293$, goats $r = -0.200$, $n = 10$), but these animals often eat the leaves off the stems rather than whole plants. Kudus tend to eat shoots or bite off whole forbs. For these animals acceptance was significantly correlated to the first factor scores in principal components analysis ($r = 0.755^*$, $n = 10$) suggesting that the proportion of ADL to nutrients in forbs was of importance to species selection by the kudus. The 'stemmy' forb species tended to be of rather low acceptance to kudus. However, the correlation was significant only due to the high acceptance of J. flava ($r = 0.315$, excluding J. flava) which is of low ADL and very high nutrient content.

I. Summary of the Chemical and Structural Basis of Species Selection by Browsing Ungulates.

i. Woody plant species which were of high acceptance to browsing ungulates were rich in protein and low in condensed tannin, and to a lesser extent ADL.

ii. There was evidence of a threshhold effect for condensed tannins. Plants containing in excess of 5% dry weight of condensed tannins in the leaves were generally of low acceptance to browsing ungulates regardless of the protein content.

iii. Condensed tannins, like lignins, are thought to be associated with plant cell wall cellulose and act to inhibit the degradation of cellulose by microbes. Ruminants are dependent upon the microbial fermentation of cellulose for much of their energy supply. Thus condensed tannins may limit the amount of energy the ruminant can obtain from the plant tissues.

iv. Neither enzyme-inhibiting polyphenols, ether-extractable fats and resins nor the major classes of toxic secondary compounds deter browsing ungulates from feeding on plants.

vi. The presence of thorns or spines reduced the rate of food intake much more for the kudus than for the impalas and goats.

v. Acacia species offering a source of concentrated nutrients, but with a very low potential intake rate, were less favoured by the kudus and goats than unarmed plants, such as G. flavescens which have leaves of similar nutrient concentration.

vi. For the impalas, which are selective leaf feeders with a rapid biting rate, the presence of thorns and spines did not affect plant species selection.

vii. The selection of forb species by browsing ungulates was not related to any chemical factor measured.

8.2. Factors of Animal Behaviour Influencing Food Selection.

A. True Browsers Versus Mixed Grazer-Browsers

Kudus are true browsers in that they obtain most of their nutritional requirements from dicotyledonous plants. Impalas and goats eat both grass and browse, thus are classified as mixed-feeders. In this study the impalas were preferential grazers of green grass in the growing season, using browse mainly in the dry season.

Since secondary chemicals are generally more common in browse than in grass it may be expected that true browsers would be more tolerant of these substances than animals which also eat grass. Laycock (1978) cites many examples of domestic grazing livestock being poisoned by plants seen to be eaten by the indigenous browsing fauna.

At Nylsvley there was little difference in the plant species selection of kudus, impalas and goats. The range of plant species seen to be eaten by the impalas was only slightly less than that of the kudus even though in the growing season the impalas ate very little browse. The goats ate some species not eaten by the kudus. This indicates that true browsers are no more tolerant of the secondary chemicals in browse than are mixed grazer-browsers.

B. Indigenous and Alien Animals

Laycock (1978) suggested that the ability to detect and detoxify plant toxins is more developed in indigenous animals, which have evolved with the vegetation, than in more recently introduced domestic animals.

One example cited, which has parallels at Nylsvley, concerns the death of sheep in Australian pastures from eating plants of the genera Gastrolobium and Oxylobium. These plants contain monofluoroacetate and are avoided by the indigenous kangaroos (Arnold & Hill 1972). In the Burkea savanna the woody geophyte Dichapetalum cymosum, which also contains monoflouroacetate, caused the death of cattle (Zimmerman 1978) and one of the goats from this study, but it was never seen to be eaten by the impalas and kudus.

Other plants eaten by the goats but not the indigenous animals were Kalanchoe species (cotyledontoxin), Asclepias species (cardiac glycosides) and Nidorella resedifolia (neuromuscular toxin - alkaloid?).

The avoidance of these toxic plants by indigenous animals may be due to "innate" behaviour or through adversive conditioning (Matthews & Kilgour 1980). Whatever the mechanism it seems that there is a difference in the ability of indigenous ungulates and domestic species to detect and thus avoid highly toxic plants.

C. Home-Range Size

Differential utilisation of the habitat may affect plant species selection. Unlike the kudus and impalas which made use of the whole 213 ha. enclosure, the four goats restricted their movement to a ten ha. home range around the water point. Such behaviour is typical of free range sheep (Arnold & Dudzinski 1978) and possibly goats as well (Schaller 1977).

The goats' home range area showed signs of depletion of the favoured browse plants by the end of the growing season. The goats began to increase their use of the 'dry season reserve' species approximately two months before the impalas and kudus did so. By the late dry season the goats were feeding extensively on the evergreen E. natalensis and leaf litter because there was very little alternative food left within their home range. When driven out of their home range into areas with more food the goats became nervous and returned to their own area at the first opportunity.

D. Supplementary Feeding

The selectivity of the goats may also have been affected by the supplement of concentrate (Epol Antelope cubes) used to lure them into a predator-proof overnight shed. Bartmann et. al. (1982) found that supplementary feeding increased the selectivity of mule deer rather than dec. asing selectivity. Results obtained for show-shoe hares when given access to commercial rabbit food were similar (Sinclair & Smith 1984). However the animals in these two

studies were g n the extra food ad libitum. The goats only received a handf f cubes each evening.

Possibly the feeding of a small amount of concentrate allowed the goats to subsist on a diet low in protein and high in fibre and possibly condensed tannins, thus allowing the goats to get by without increasing their home range size.

E. Summary of Factors of Animal Behaviour Influencing Food Selection

i. The range of browse species eaten by true browsers (kudus) was no greater than that eaten by mixed-feeding species living within the same habitat.

ii. Domestic goats were less able to recognise, and hence avoid, the few highly toxic plant species occurring in the Burkea savanna than were the indigenous ungulates.

iii. The greater use of E. natalensis by goats than impalas and kudus in the dry season may be as a consequence of resource depletion within the small home range of the goats or as a consequence of limited supplementary feeding of concentrates to the goats.

8.3. Plant Defences Against Herbivory

The possession of defensive compounds and structures represents an

energetic and nutritive cost to the plant, as resources for defence are diverted from growth and reproductive potential (Hanover & Hoff 1966, Foulds & Grime 1972, Mothes 1976, Pimental 1976, Chew & Rodman 1979, Rhoades 1979). Thus plants should allocate defensive compounds in a way that provides an adequate level of defence but at a minimum metabolic cost.

A. The Theory of Apparency

In 1976 Feeny and Rhoades & Cates independently proposed that the degree of defensive commitment by a plant was directly related to the risk of its discovery by herbivores. Plants under a high risk of predation should have a greater allocation of metabolites to defence than those species which may escape discovery either temporally or spatially. The former "apparent" plants were taken to be woody perennials, especially evergreens, common and late sucessional species. The latter, "unapparent" plants included herbaceous species, deciduous, rare and early sucessional plants. Tissues such as new leaves were also considered to be unapparent to herbivores as they are available only for a short time.

The distribution of digestion-reducing and toxic defences was related to plant apparency. Digestion-reducing compounds were regarded as being expensive to the plant's metabolism as they are effective only in large quantities, but are effective against both generalist and specialist herbivores. Toxins, on the other hand, are effective in minute amounts, but can be overcome by specialist herbivores. Thus they were considered as being cheap,

but less effective than digestion-reducing compounds (Feeny 1976, Rhoades & Cates 1976).

Plant-parts valuable to the plant, in terms of fitness lost should they be eaten by herbivores, were expected to be protected by expensive, digestion-reducing compounds while less valuable tissues, or those with a low risk of discovery by herbivores were expected to be defended by cheap toxins.

At Nylsvley the distribution of digestion-reducing and toxic defences between woody plants and forbs was as predicted by the apparency theory. Digestion-reducing tannins were prevalent in the woody vegetation, while alkaloids occurred mainly in the forbs. Intermediate compounds, such as terpenes and saponins, having both toxic and digestion-reducing properties, occurred in both woody plants and forbs.

All the plant species analysed for chemical factors were common species but within the woody component the very abundant and evergreen plants should have a greater allocation to digestion-reducing substances than the less common species.

The dominant woody species of the Burkea savanna, B. africana, O. pulchra and T. sericea (Rutherford 1982) were of high condensed tannin content. In the Acacia savanna the dominant plants contained lower levels of condensed tannins but A. nilotica and D. cinerea were rich in enzyme-inhibiting polyphenols. The third species A. tortilis was of average phenolic content, yet was

equally as apparent to herbivores as A. nilotica and D. cinerea.

Of the two common evergreen species E. natalensis was, as predicted by the apparency theory, rich in condensed tannins but the other common evergreen, S. pungens, contained no condensed tannins; instead it was one of the few woody plant species to contain alkaloids throughout the year. Neither species contained high concentrations of enzyme-inhibiting polyphenols.

New leaves are only available to herbivores for a short time, therefore are considered "unapparent". As such the allocation to defensive compounds should be less.

There was little evidence of toxic defen es in new leaves of the woody plants at Nylsvley. Only D. rotundifolia and T. sericea leaves reacted positively with alkaloid detection reagents. Saponins although classified as toxins were generally less abundant in immature leaves.

Concentrations of enzyme-inhibiting polyphenols were slightly lower in the new leaves of most species but in C. molle and P. africanum approximately 20% of the dry weight of immature leaves was attributable to enzyme-inhibiting polyphenols. Thus the distribution of defensive compounds in new leaves at Nylsvley does not really fit the predictions of the apparency theory.

As more studies of plant defensive allocation are done, the more exceptions to the apparency theory are found, and the

distribution of digestion-reducing and toxic compounds becomes less clearly separated. In tropical forests the young leaves of many trees contain similar, or even greater, quantities of digestion-reducing compounds than the mature leaves (Mi'ton 1979, Gartlan et. al. 1980, Coley 1983).

Studies of the synthesis and maintenance of tannins, terpenes and alkaloids suggest that the differences in the turnover rate of these compounds may greatly reduce the differences in metabolic costs of digestion-reducing and toxic compounds (Swain 1979), but even within groups of compounds the turnover rate is highly variable (Prudhomme 1983).

The distinction between the action of the quantitative or digestion-reducing and qualitative or toxic defensive compounds is also blurring.

This study alone has shown that enzyme-inhibiting polyphenols, although present in high concentrations in many plants, do not deter browsing ungulates, nor are the plants rich in condensed tannins free from insect attack. Many other studies have also found that certain digestion-reducing compounds fail to protect the plant against some herbivores, and especially certain insects (Fox & Macauley 1979, Bernays 1978, 1981, Bernays & Woodhead 1982).

In a study of the comparative defensive chemistry of pioneer (unapparent) and persistant (apparent) species in a Panama rain

forest Coley (1983) found no evidence of new leaves escaping herbivory by insects by temporal predator saturation through synchronous flushing, nor did gap-colonising pioneer plants escape herbivory by spatial distribution. Pioneer plants in fact suffered heavier defoliation than persistents due to specialist insects. The theory of apparency did not consider that once a specialist feeder has found a plant it can remain on the plant and inflict prolonged damage. Whereas a generalist feeder cannot stay on one plant for long, but moves around from plant to plant, thus causing a more even distribution of damage among individuals of a particular species. Due to the mobility of generalist feeders rare plants will be damaged just as much as common plants.

Browsing ungulates are generalist feeders. The kudus, impalas and goats fed for only two or three minutes on any one plant before moving on to different species. Even in the late dry season, when food availability was low, plants were never totally defoliated in one feeding bout.

Rare plants did not escape herbivory by the browsing ungulates. Few plant species were never seen to be eaten. Although not evident in this study many browsers have been shown to feed selectively on rare plants (Milton 1979, Oates et. al. 1980, Waterman et. al. 1980, Glander 1981). Thus mammalian herbivores tend to put the greatest browsing pressure on the rare plants. Hence the theory that rare plants escape herbivory by generalist feeders, does not apply to large herbivores.

B. Soil Nutrient Status

Plants growing on nutrient poor soils have a low productivity. This implies a slow growth rate and prolonged life cycle. The plants are therefore vulnerable to discovery and attack by herbivores. Janzen (1974) proposed that the investment in defensive compounds should be greater for plants growing in nutrient poor soils than in more fertile soils, due to the higher metabolic cost of replacing tissues lost to herbivory.

Evidence in support of this hypothesis was established by McKey et. al. (1978) in a study of two African rain forests. Trees from the Cameroons forest, growing on acidic white sands of low nutrient availability, contained higher levels of phenolic compounds than trees from the more fertile Ugandan site. Further investigation by Gartlan et. al. (1980) revealed that although the phenolic content of trees in the nutrient poor site was more than double that of the vegetation in the more fertile site, alkaloid containing trees were less common.

At Nylsvley the vegetation was a mosaic of Burkea savanna and smaller patches of Acacia savanna. The Burkea savanna grows on dystrophic sandy soils (ph 5.0, cation exchange capacity 0.3-0.6 me/100g, available phosphorus 2-10 ppm). Acacia savanna occupies patches of slightly more fertile soils (ph 6.0, cation exchange capacity 1.6 me/100g, available phosphorus 7-42 ppm) (Harmse 1977, Knoops 1982).

Following Janzen's (1974) prediction the plants of the Burkea savanna should have a higher commitment to defence than those of the Acacia patches. The dominant woody plants of the Burkea savanna did contain higher concentrations of condensed tannins than plants in the Acacia patches, but there was no significant difference in the average content of enzyme-inhibiting polyphenols in the vegetation of the two savanna types.

This suggests a rather different role for these two types of tannins in the plants. Condensed tannins function to inhibit the degradation of plant cell walls by microbes. Thus as well as functioning in disease resistance and deterring browsing by ruminant herbivores high concentrations of condensed tannin will limit the rate of nutrient release from leaf litter (Swain 1979, Zucker 1983). This function could be of greater importance to plants growing in nutrient poor soils than plants growing in more fertile environments. The deterrent effect of condensed tannins upon ruminant browsers may even be a secondary consequence of their function in inhibiting penetration of the tissues by free-living microbes.

C. Habitat Quality and Plant Growth Rate

The availability of soil nutrients is one of several factors controlling the growth rate of plants. Coley (1983) suggested that potential growth rate is the factor governing a plants commitment to growth.

In a Panama rainforest the growth rate of pioneer plants was 2.5 times that of persistents. The leaves contained less fibre and defensive compounds and were shorter-lived than those of persistents. Since the leaves of pioneers were cheaper to replace than the fibrous, heavily defended leaves of persistents, such plants could withstand a greater unit loss to herbivory than could the slow growing species. Thus potential growth rates influence the plants' commitment to defence. The advantages of defence should increase as the potential for growth declines.

As yet there has been no comprehensive study of the growth rate of woody plants at Nylsvley, or in any other savannas. Seedlings of Acacia species grew much faster than those of B. africana, which in turn grew faster than those of E. natalensis (Bryant pers. comm.) but it is not known how this relates to the growth rate of established plants.

Both of the slow growing species, B. africana and E. natalensis, contained high levels of condensed tannins. The Acacia species contained much lower concentrations of condensed tannins, but A. nilotica leaves were very rich in enzyme-inhibiting polyphenols, up to 30% of the dry weight of the leaves comprised polyphenols. A third rapid growing plant T. sericea was rich in both enzyme-inhibiting polyphenols and condensed tannin as measured by the proanthocyanidin method. This species was of higher acceptance to browsing ungulates than the other species rich in condensed tannins. It is possible that some

of the compounds measured as condensed tannins in this plant were infact unconjugated precursors of condensed tannins, thus would not have the same inhibitory effect upon microbes, but even so such compounds are not primary metabolites in plants. This suggests that a rapid growth rate does not necessarily correlate wich a lower investment in secondary compounds than in more slowly growing plants.

D. The Carbon / Nutrient Balance of Plants

It has recently been proposed that the degree and type of defensive commitment is a function of the carbon / nutrient balance of the plants (Bryant et. al. 1983, Prudhomme 1983). The carbon / nutrient balance is dependent upon environmental constraints and the potential growth rate of the plant.

Plants rarely photosynthesise to their greatest capacity as nitrogen is more often limiting to the growth of plants than carbon (Krischik & Denno 1983). Plants that occur in nutrient poor soils have an intrinsically slow rate of growth. These plants will have a greater excess of carbon from photosynthesis than more rapidly growing plants on soils of greater nutrient availability (Mattson 1980, Bryant et. al. 1983). For nutrient limited plants with an excess of photosynthate carbon-based deterrents will be cheap relative to compounds like alkaloids which contain nitrogen. However, even carbon-based defences require enzyme systems for their synthesis, so do have a nutritive cost to the plant (Mooney & Gulman 1982).

The extreme form of slow growing plants are the evergreens. These plants store most of their nutrients and energy in the leaves thus avoiding the often heavy costs of translocation (Penning de Vries 1972, Chapin et. al. 1980). Since the plant stands to lose much of its stored nutrients each time a leaf is shed, the leaves are long-lived (Chapin 1980). Long-lived leaves are likely to encounter unfavourable environmental conditions, such as water deficit, are highly fibrous and have a thick cuticle. The leaves are also susceptible to attack by herbivores and pathogens so tend to have a heavy commitment to defensive compounds (Bryant et. al. 1983).

Rapid growing plants on fertile soils tend to have short lived, deciduous leaves and more below ground reserves for compensatory growth. The plant therefore does not require such heavy defences against herbivory. The nutrient stores also allow the plant to use facultative defences rather than constitutive defences as required by slow growing plants.

At Nylsvley the soils are classified as dystrophic (Harmse 1977), and are of low nitrogen content (0.25 - 0.45% in Burkea savanna, 0.42% in Acacia savanna). Thus it is expected that the plants should be slow growing and have a strong commitment to carbon-based phenolic and terpenoid compounds rather than defensive compounds containing nitrogen.

As a general trend the theory of carbon / nutrient balance holds at Nylsvley. Tannins were abundant in many of the woody plant species, alkaloids were rare and cyanogenic glycosides absent from the species analysed.

The biomass of consumers was greater in the Acacia patches, typical of arid, eutrophic environments than in the Burkea savanna associated with the mesic, dystrophic savannas of Africa (Huntley 1982). This was associated with the greater nutrient content and lower proportion of structural carbohydrates in the vegetation of the Acacia savanna.

At the species level the carbon / nutrient balance theory is less successful. The three dominant tree species of the Acacia savanna all have nitrogen-fixing root nodules (Grobelaar & Clarke 1975) and occur on soils of slightly enriched nutrient status (Coetzee et. al. 1976). These plants should have more nutrients for growth and therefore less excess carbon for defence than plants of the Burkea savanna. All three species had average or low condensed tannin contents, yet both A. nilotica and D. cinerea contained high levels of enzyme-inhibiting polyphenols in excess of concentrations found in the majority of Burkea savanna plants analysed.

Not all the species growing on the dystrophic Burkea savanna soils were of high tannin content. G. flavescens, R. leptodictya and V. rehmannii were low in tannins. The latter two species contained aromatic compounds, while G. flavescens is locally

abundant, occurring mainly on old ant-hills, indicative of a possible microsite difference.

According to the theory evergreen plants are slow growing and have strong chemical defences. E. natalensis was a typical species having fibrous leaves rich in condensed tannins, but the other evergreen S. pungens contained little phenolic defences. Instead this species had hard, stiff leaves armed with terminal spines. Possibly the excess carbon in S. pungens was diverted into structural defensive fibre and spines rather than digestion-reducing compounds. This was also one of the few woody plant species to react positively to alkaloid detection reagents. However, compared to forbs the reaction was weak.

Forbs grow on the same soils as woody plants yet contained alkaloids rather than tannins. Coley (1983) invoked microsite differences to explain the differences between the defensive commitment of forbs and woody plants, but there is no evidence for this. Forbs are generally fast growing plants (Johnson & Teiszen 1976) and as such should have less excess photosynthate for defence. Also being shallow rooted they are more prone to water stress than deeper rooted woody plants. Wilting of forbs was commonly observed at Nylsvley. Water deficit may limit carbon availability to the forbs through stomatal closure.

Forbs may tend to use qualitative defences rather than digestion-reducing compounds as these can easily be transferred from the leaves to the seeds as the value of these tissues to the

plant varies, hence giving the plant protection where it is most needed at a minimal cost to potential growth (McKey 1979).

In addition, digestion-reducing compounds are only effective in large quantities. Annuals plants growing from seed cannot draw on stored carbohydrates for such defences as can perennial species. However, no difference was evident between the defensive allocation of annual and perennial forbs at Nylsvley.

E. Summary: The Allocation of Metabolites to Defence in Savanna Plants

i. The woody plants at Nylsvley contained high concentrations of phenolic compounds, while alkaloids were the prevalent defence in forbs. Terpenes and saponins, which have both toxic and digestion-reducing properties, occurred in both woody plants and forbs. This distribution of defensive compounds is as predicted by the theory of apparency (Feeny 1976). At the species level this theory was less sucessful.

ii. That the defences of the woody plants at Nylsvley should be based on carbon, was predicted by several of the current theories invoking soil nutrient status, habitat quality and the carbon / nutrient balance of the plants. Yet none adequately explains why species of the Acacia savannas, which are of rapid growth rate and occur on soils of enhanced nutrient status, should contain equally high or even higher concentrations of tannins than the slow growing plants of the

Burkea savanna.

iii. The differences in the defensive allocation of Acacia and Burkea savanna plants was not in the quantity of tannins but in the action of these compounds. Plants of the Burkea savanna contained higher concentrations of condensed tannins than occurred in Acacia savanna species, in which the predominant tannins were the enzyme-inhibiting polyphenols or hydrolyzable tannins.

iv. The action of condensed tannin is threefold, in reducing leaf loss to ruminant herbivores, in disease resistance and in slowing down rates of nutrient loss from leaf-litter.

v. Plants of slow growth rate require greater protection against leaf loss than do rapidly growing species for which replacement of leaves is less of a drain on the metabolism of the plant. Loss of nutrients by leaching is also more detrimental to plants growing under conditions of low nutrient availability. The high concentrations of condensed tannins in Burkea savanna species provide this protection.

vi. Although they grow in the same soils as the woody plants forbs in savannas tend contain much higher concentrations of nitrogenous defences such as alkaloids. This may be as a result of higher nutrient availabilities in the surface layers of the soil, a lack of stored carbon in plants growing from seed, or from the fact that it may be more economical for short lived plants to utilise defences which are easily

translocated to the tissues most in need of defence.

8.4. The Relative Impact of Plant Tissue Losses Due to Vertebrates, Invertebrates and Fire

There are three main defoliation agents in savannas, fire, vertebrate herbivores and invertebrates.

Savannas are fire dominated communities (Huntley 1982). The evergreen growth form is associated with low soil nutrient availability (Chapin 1980) yet few evergreen species occurred at Nylsvley or in other African savannas (Huntley). The low abundance of evergreen plants is also a feature of South American savannas (Medina 1982). In a fire, evergreens stand to lose a large proportion of their nutrients. The few evergreen plants in Bazilian savannas have been found to be particularly deep rooted, so have an advantage over shallower rooted plants when moisture is limiting (Medina 1982). Deciduous plants retract nutrients from their leaves before abscission (Bate & Gunton 1982) so when fires sweep through the vegetation in the dry season these plants lose a minimum of nutrients. Fire adapted and deciduous plants have large nutrient reserves in the roots for rapid regrowth (Garrison 1972).

This raises the question as to how damaging is herbivory to savanna plants which can exist under a fire regime?

Fires defoliate plants mainly in the dry season when the

plants are dormant. The fires also tend to sweep through the grass layer, so affect small plants more than those which have grown above the grass layer.

Herbivores are active throughout the year, removing photosynthetically active tissue and hence may have a greater effect upon plant fitness than fire.

At Nylsvley, when cattle were present, vertebrate and invertebrate herbivores removed similar proportions of the annual production of grasses and forbs. Approximately 42% of the grass and 28% of the forb production was removed each year. Without cattle only 11% of the herbaceous layer was consumed but this was due to a simultaneous reduction in the number of grasshoppers (Gandar 1982).

The proportional consumption of woody plant leaves was much less than for herbaceous plants. Only 4.5% of the annual production of leaves was eaten. Invertebrates, in particular lepidoptera larvae, accounted for twice as much biomass removal as vertebrate herbivores, mainly kudus.

Outbreaks of defoliating catepillars are intense and localised. Unlike vertebrates insects tend to have a high degree of host specificity. Defoliation is often early in the growing season and can result in a poor or aborted seed crop (Rhoades 1983).

Herbivory by vertebrates is of low intensity throughout the year, but due to the size of individual herbivores, can be intense for individual plants. Vertebrates are usually generalist feeders spreading their utilisation over many individual plants of many species. Plants may also grow out of the height reach of most vertebrate herbivores present in savannas. Only in certain circumstances can vertebrate herbivores significantly alter the composition of the woody component of savannas (Du Toit 1972).

8.5. The Relative Impact of Herbivores and Pathogens on the Defensive Chemistry of Plants

At Nylsvley herbivory only removed an estimated 4.5% of the annual leaf tissue produced by woody plants (Gandar 1982). Plants may suffer loss of fitness not only through tissue removal by herbivores but also loss of photosynthetic potential due to attack by microbial pathogens. While plant secondary compounds are not universal deterrents to herbivorous animals many are reported to have anti-microbial properties (McKey 1979), either through poisoning the microbes like terpenes (Oh et. al. 1967) or obstructing their entry into the cells as is the ability of condensed tannins and lignins (Swain 1979). Possibly the major target of plant defensive compounds is against microbes, the effect on ruminant browsers being secondary via the effect upon the symbiotic rumen flora.

Wound induced production of phenolic compounds is fairly common in trees of temporate woodlands (Haukioja & Niëmala 1976

1979) but has only been tentatively described in savanna plants (Van Hoven 1984). The function of this response may not be to reduce herbivore feeding as much as to seal the open tissues against possible invasion by microbial pathogens.

8.6. SUMMARY

i. Tannins were the most abundant defensive compounds in the woody plant species of the Acacia and Burkea savannas at Nylsvley. Terpenes and saponins were common but alkaloides and cyanogenic glycosides were rare. Forbs contained alkaloids, terpenes and saponins but little tannin.

ii. No defensive compound gives the plant protection against all classes of herbivore. Condensed tannins appear to be the only major group of defensive compounds deterrent to browsing ruminants, yet plants containing high concentrations of these compounds in the leaves suffer periodic outbreaks of defoliating caterpillars.

iii. Several theories of plant defensive allocation predict that the slow growing plants on the dystrophic soils of the Burkea savanna should have a greater commitment to carbon-based defences than the faster growing plants on the nutrient enriched soils of the Acacia savanna. This was not so, however the type of tannins prevalent in the two savannas differed. The dominant species of the Burkea

savanna contained high concentrations of condensed tannins while the Acacia savanna species contained more enzyme-inhibiting polyphenols.

iv. Condensed tannins are associated with plant cell walls and function to protect against penetration by microbes. This property confers resistance to attack by bacterial and fungal pathogens, inhibits microbial fermentation of plant material by the symbiotic microflora of the rumen thus rendering the plant a poor source of energy to ruminant herbivores, and also decreases the rate of litter breakdown and consequently nutrient release. All these properties make condensed tannins useful to plants growing under conditions of low nutrient availability. Even high concentrations of enzyme-inhibiting polyphenols did not deter feeding by browsing ungulates. Possibly these compounds are active against the digestive enzymes of insects.

v. Plant species selection by browsing ungulates appears to be a series of negative decisions. Any woody plants containing particularly toxic compounds, or having a condensed tannin content above 5% dry weight in the leaves, are unlikely to be eaten. Of the species free of these defensive compounds those with high nitrogen, i.e. protein, contents are preferred over more fibrous species. No clear selection for minerals was evident, however most of the protein rich plants tended to be of high mineral content. In the dry season when the availability of the favoured deciduous

species declined the animals relaxed their selective criteria. First they increased their acceptance for the more fibrous species and only at the end of the dry season were those species containing high concentrations of condensed tannins eaten.

vi. The presence of structural defences on the plants, especially when combined with a small leaf size, limited the bite size of the animals to single leaves. This was to some degree compensated for by an increase in the biting rate of the animals but still the intake rate of the animals was less than that from unarmed species. This effect was particularly strong for the kudus. Armed species tended to be of rather lower acceptance to the kudus than unarmed species of similar nutrient content.

vii. Although the presence of thorns does not prevent large herbivores from eating the leaves of plants, the plant benefits from a reduced rate of leaf loss when browsed. The leaves of the armed species were often of nigh nutrient content, but also there was no obvious decrease in the commitment to chemical defences. Thorns only protect the plant from one category of enemy, further defences are needed against insects and microbial pathogens.

viii. Other than the avoidance of a few highly toxic species the selection of forb species could not be related to chemical factors. A great variety of forb species were eaten in small amounts. The generalised diet of large herbivores is

possibly a mechanism for the avoidance of ingesting any one toxin in deleterious amounts rather than a means of obtaining a balanced intake of nutrients, since proportions of nutrients in different plant species are similar.

ix. Basically the plant species selection patterns shown by kudus, impalas and goats were similar. Selection for and against various chemical factors was shown most clearly by the kudus. The patterns were less clear for the mixed grazer-browsers which obtain much of their food from grass. Slight differences in the seasonal acceptance of plant species by the goats were attributable to their remaining within a small home range and to their apparent inability to detect and avoid some of the more toxic plant species.

CHAPTER 9.

PRACTICAL IMPLICATIONS OF THIS STUDY

Savannas cover 65% of the African Continent and over 30 million hectares of South Africa (Huntley & Walker 1982). Crop production in the more arid savannas is unreliable due to the low and erratic rainfall. The cost of bush clearance plus irrigation is often uneconomical (Walker 1980). Such regions are used mainly for extensive livestock ranching. Cattle ranching is the main use of Burkea savanna, but is not very profitable due to the low carrying capacity of the land (8 - 10 ha/au/yr), and to the presence of the poisonous woody geophyte Dichapetalum cymosum (Grunow & Grossman 1982).

Current rangeland practices have led to bush encroachment, and hence a reduction in grass cover, leading to decreased livestock production and increased soil erosion. This situation is ascribed by Aucamp (1976) to the use of only bulk grazers, namely cattle. The grass component is stressed by heavy grazing pressure. This reduces its competitive ability against the woody components which in present rangeland systems is relatively unused.

It has been suggested that the use of browsers in savannas could potentially retard bush encroachment and substantially increase meat production in the more arid regions (Aucamp 1978, Donaldson 1979, Walker 1979, 1982, Du Toit 1981, Aucamp et. al.

1984).

The use of browsers in bush control is limited. The animals can only affect palatable plants within their height reach. Goats can decrease the cover and density of small woody plants in Mopane veld (Donaldson 1978), leading to a better grass cover and increased production of cattle. The inclusion of indigenous browsers in cattle ranching also resulted in a lowering of the density of small woody plants in arid savannas (Taylor & Walker 1978). Continual browsing by goats can supress reinvasion by Acacia karoo from seed reserves following bush clearance (Du Toit 1972). The goats only browsed new twigs and hence could not control established plants.

Where browsers are to be used for sustained meat yield the stocking rates are low compared to cattle. This is attributed to the physical unavailability of much browse material (Donaldson 1978, Aucamp & Dankwerts 1984), and to the slow recovery rate of many woody plants after browsing and the low availability of browse in the dry season.

From this study it must be added that much of the physically obtainable browse is physiologically unavailable to browsers due to high concentrations of indigestible fibre and plant secondary compounds, in particular condensed tannins. In dystrophic savannas the dominant plants are often of little use as food for browsers. In this study the ecological dominants of the Burkea savanna B. africana, T. sericea and O.pulchra were of high condensed tannin

content. The dominant species Colophospermum mopane of Mopane savanna and Brachystegia spiciformis of Miombo savanna are also of low palatability to browsers (Martin 1974, Walker 1982). In the more eutrophic Acacia savanna the ecological dominants are of higher acceptance to browsers.

Identification of potential food plants for browsers usually stems from direct observations. Due to the great seasonal change in use of browse plants these studies are time consuming and usually relate only the habitats in which that particular mix of species occurs. This study offers a rapid identification of the plants of little use as food to ruminant browsers. Such species will contain over 5% dry weight condensed tannin in the leaves, relative to a Sorghum III tannin standard. This can be easily assessed by the Bate-Smith proanthocyanidin test (1977). Preparation of the plant extract is time consuming but the test is simple and uses no expensive reagents. Automated systems for rapid analysis of tannins have been developed (Bryant pers. comm.) but were not available for this study. Plants containing less condensed tannin than the threshhold value are likely to be either preferred or dry season reserve foods. Preferred plants are distinguished from reserve species by their high protein and low fibre content. Analysis of protein contents is a routine procedure in most nutritional laboratories. Fibre analysis is more costly and time consuming, but since protein is inversely correlated to fibre it is not neccessary for both tests to be done

There is much overlap in the plant species preferences of

browsing ungulate species, but the larger browsers such as kudus tend to make less use of small-leaved thorny plants, from which the bite-size achieved is restricted in size, than do more delicate feeders like impalas. The small leaved Acacia species are often invasion cleared pastures. Their growth is more likely to be retarded by small browsers such as goats than by kudus.

Impalas are preferential grazers of green grass, eating significant quantities of browse only in the dry season. Much of this browse is eaten as single or fallen leaves. Impalas therefore are unlikely to have much effect upon woody plants in areas where grass is available. Also they may compete with cattle for grass in the growing season. Goats are also mixed feeders but use more browse than impalas in the same habitat. They cause more damage to the woody component as they bite off terminal shoots as well as leaves, and frequently break down branches with their forefeet while feeding. Kudus eat more browse than either impalas or goats. They eat mainly shoots and break down branches in the dry season.

Goats have the advantage in agricultural systems of being easy to herd and market. They are fecund animals often producing twins. In savanna rangelands boer goats can produce more red meat per unit metabolic weight than sheep or cattle, and in the thornveld areas of the Karoo can select a rich enough diet to grow throughout the year (Aucamp et. al. 1984). The Burkea savanna is less fertile than the Acacia thornveld (Harmse 1977) so production may be less than that recorded in the Karoo. The disadvantages of using goats are their high susceptibility to tick-borne diseases,

predation and poisoning by toxic plants (Barnes 1982). In this study all these problems were encountered. Where such conditions prevail, as in the Burkea savanna, indigenous browsing ungulates could be used.

Little is known of the conversion efficiency in kudus, but impalas have a daily mass gain just slightly better than that of cattle but their food conversion efficiency is 3.8% instead of 5% for cattle. However, this figure included the production of fat by cattle (Skinner et. al. 1983).

Problems in farming with wild animals include meat spoilage in culling operations, market limitations, veterinary restrictions and the inability to herd wild animals. The additional cost of game fencing must also be taken into account.

CHAPTER 10.

CRITIQUE OF THE PROJECT

i. Goats

The feeding behaviour of the goats may have been modified by the need to lock them in a leopard-proof shed at night. The free ranging animals often fed at night during hot weather.

The goats were enticed into their shed with a small quantity of 'Epol' antelope cubes, The feeding of this concentrate may have allowed the goats to subsist on a very low protein high fibre diet in the late dry season.

The goats chose to remain within a small home area in which browse became depleted. The kudus and impalas used the whole enclosure. It may have been better to herd the goats into the veld as an agricultural system. This however imposes some degree of human choice into the habitat selection of the animals.

ii. Chemical Analysis

The measurements of the presence or absence of maj. groups of toxins in the plants is inadequate. Such a wide range of biological activity exists within each major group that no pattern of selection could be detected at this level. Condensed tannins

turned out to be the most important category of secondary chemicals in woody plants as far as selection by browsing ungulates was concerned. Yet concentrations were only measured in mature, green leaves. This arises from a misunderstanding by the chemists contracted to analyse for these tannins; polyphenols being measured instead. It was intended for the researcher to analyse samples of immature and old leaves for condensed tannins but there was insufficient time before the project had to be completed.

iii. Sample Size

Had it been economically feasible more plant species should have been analysed for their chemical contents. With only 10 or 14 species regressions can be dominated by one or two species. As it was even the number of analyses originally planned had to be reduced due to recurrent staffing problems at the analytical laboratories.

CHAPTER 11.

FURTHER INFORMATION NEEDED

i. Investigation of Condensed Tannins in Browse Plants

A more detailed investigation of the tannins in browse plants may reveal whether or not they do exist solely as cell-wall bound molecules or whether some of that measured as condensed tannin is in fact flavonoid precursors which polymerise on drying, as found in Alaskan Birch (Bryant pers. comm.). Such percursors are removed from the plants by extraction with ether prior to testing for condensed tannins.

ii. Digestibility Trials

This study has revealed that the major factors influencing the consumption of woody plants by browsing ungulates are cell wall bound condensed tannins, and possibly lignin. These compounds are assumed to inhibit the fermentation of cellulose by the rumen microflora. Digestibility trials using plants of known tannin and lignin contents would resolve this point.

iii. Insect Herbivores

Plants containing high concentrations of condensed tannins are not favoured by browsing ungulates but do suffer periodic outbreaks of

defoliating insects. The mechanics of pest outbreaks in temperate tree species is usually stress (Rhoades 1983). Insect defoliation of savanna trees may follow chemical changes induced by stresses, such as drought, but this remains to be investigated.

iv. Facultative Defence

The majority of savanna plants are fire tolerant deciduous species. As such they are presumed to have large root reserves for rapid regrowth following defoliation (Menaut & Cesar 1982). This is supported by observations of reflushing after insect defoliation but has not been proven. Plants with large nutrient reserves may use facultative defences against defoliation. Whether or not this phenomenon is common in savanna plants, the compounds involved and response times remain to be investigated through clipping or controlled herbivory experiments.

v. Growth Rate of Savanna Plants

The commitment of a plant to defence is thought to be related to the carbon / nutrient balance of the plant, including soil nutrient availability and potential growth rate. As yet no study of the relative growth rate of savanna plants has been undertaken. Studies of rate of extension of twigs are inadequate as they do not relate between species to seasonal biomass increment.

vi. Plant Responses to Browsing

In order to achieve the optimum long term stocking density of browsers in nature reserves or agricultural rangelands it is essential to know the effect browsing has on the growth, reproduction, recruitment and survival rates of browse species. Such a study is being carried out at the Nylsvley Nature Reserve and Umfolozi Game Reserves by O'Regan, under the South African Savanna Ecosystem Project.

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APPENDIX 1

Appendix 1.

The Composition of "Epol" Antelope Cubes

Yellow Maize Meal	70%
Wheat Bran	17%
Sunflower Cake Meal	5%
"Rumevite"	5%
Mineral lick	3%

APPENDIX 2

Appendix 2.

The Composition of the Mineral Lick

Bone Meal	30 kg
Sodium Chloride	15 kg
Manganese Sulphate	120 gms
Copper Sulphate	60 gms
Cobalt Sulphate	15 gms
Sodium Iodide	5 gms

Appendix 3.

The Proportions of the Major Vegetation Components in the Diets of Browsing Ungulates.

i. Kudus

Month	n	Grass	Woody Browse	Forbs	Leaf Litter	Fruit	Other
1981		Mean SE	Mean SE	Mean SE	Mean SE	Mean SE	Mean SE
October	5	3.18± 1.38	67.42± 6.68	17.24± 9.64	- -	12.12± 3.42	- -
November	5	5.20± 2.67	52.18±11.29	33 30± 9.87	- -	9.32± 6.50	- -
December	9	18.19± 2.88	58.14± 4.98	22.88± 5.55	0.87± 0.87	8.69± 8.68	- -
1982							
January	6	28.40± 7.66	55.65±13.44	16.62± 4.18	- -	7.33± 7.17	- -
February	6	8.10± 3.13	76.23± 6.84	12.62± 2.31	- -	3.02± 2.21	- -
March	7	5.74± 3.38	56.49± 8.56	18.63± 4.94	- -	19.14± 9.65	- -
April	6	18.65± 3.85	46.37±11.76	28.58± 5.85	- -	22.48± 7.59	- -
May	6	4.17± 2.17	54.13± 5.37	22.82± 2.23	- -	19.68± 5.21	- -
June	2	8.08± -	31.48±22.58	2.48± 8.18	- -	66.28±22.48	- -
July	6	8.08± -	72.97± 7.13	11.95± 2.96	9.47± 4.89	5.62± 2.89	- -
August	7	8.10± 8.87	61.81± 8.47	11.65± 3.22	12.49± 4.88	13.68± 7.17	1.54± 1.54
September	4	3.55± 1.99	65.63±15.14	2.35± 1.23	- -	17.63± .28	18.85± 8.21

Appendix 3.

The Proportions of the Major Vegetation Components in the Diets of Browsing Ungulates.

iii. Goats

Month	n	Grass	Woody Browse	Forbs	Leaf Litter	Fruit	Other
1980		Mean SE	Mean SE	Mean SE	Mean SE	Mean SE	Mean SE
December	4	47.75± 4.28	42.75± 8.18	9.60± 6.33	- -	- -	- -
1981							
January	7	17.29± 9.66	77.71± 9.59	2.39± 1.44	- -	2.61± 2.36	- -
February	5	18.78±4.87	47.83±16.26	22.78± 9.79	6.14± 6.14	8.88± 8.88	- -
March	4	20.88±11.25	36.48± 9.23	22.13± 7.78	12.43± 7.18	8.25± 8.25	- -
April	5	8.88± 8.85	26.48± 5.77	7.76± 8.99	61.86± 3.56	9.90± 2.52	- -
May	7	7.63± 2.11	21.14± 6.61	8.45± 4.52	47.38± 7.90	6.57± 3.35	- -
June	6	3.42± 2.85	38.98± 4.65	25.33± 8.69	34.45±12.86	2.88± 0.78	5.82± 4.72
July	7	4.69± 1.45	37.13± 6.85	6.61± 2.55	48.73± 6.88	1.83± 0.52	1.83± 1.45
August	6	1.95± 0.46	49.62± 6.99	5.20± 2.70	29.08± 5.23	10.65± 4.66	2.60± 2.68
September	6	20.85± 5.32	43.88± 6.59	18.78± 6.81	13.85± 4.38	11.20± 4.78	1.87± 0.87
October	6	16.64± 5.21	61.78± 5.89	18.24± 3.25	7.73± 1.87	2.18± 0.78	1.58± 1.44
November	6	19.83± 6.94	52.48± 5.33	8.13± 2.51	2.75± 0.84	17.33± 8.78	8.35± 8.35

Appendix 3.

The Proportions of the Major Vegetation Components in the Diets of Browsing Ungulates.

ii. Impalas

Month	n	Grass	Woody Browse	Forbs	Leaf Litter	Fruit	Other
1980		Mean SE	Mean SE	Mean SE	Mean SE	Mean SE	Mean SE
October							
November							
December	7	88.84± 3.56	14.73± 2.89	4.43± 1.43	- -	- -	- -
1981							
January	6	79.72± 7.91	15.62± 7.86	4.67± 2.37	- -	- -	- -
February	5	73.68±5.81	16.46± 1.57	10.46± 5.91	- -	- -	- -
March	3	41.97± 2.82	55.80± 3.87	2.23± 2.23	- -	- -	- -
April	4	34.48± 9.90	35.98±12.71	29.63± 6.68	- -	- -	- -
May	6	53.38±15.94	1.23± 0.71	14.77±10.24	19.58±12.25	11.23± 8.12	- -
June	6	15.82± 3.47	24.72±10.60	18.25± 8.53	36.97± 9.78	4.25± 2.78	- -
July	7	17.16± 5.94	3.81± 1.28	8.48± 1.31	59.89±18.28	11.79± 8.19	- -
August	6	58.54±14.86	2.43± 0.96	2.43± 1.85	38.77±12.81	5.80± 2.93	0.12± 0.12
September	5	92.14± 4.66	2.48± 2.86	0.82± 0.82	5.16± 4.87	- -	- -
October	5	61.76±3.43	27.82± 6.46	10.64± 6.14	0.82± 0.82	- -	0.78± 0.78
November	5	73.80± 9.46	15.28± 4.62	10.28± 6.54	0.86± 0.86	0.22± 0.22	0.36± 0.36
December	6	88.48± 4.87	13.92± 2.62	3.12± 1.94	1.18± 0.69	- -	1.38± 0.71
1982							
January	6	91.43± 4.24	7.58± 3.77	0.32± 0.16	0.23± 0.16	0.35± 0.35	- -
February	5	72.58± 3.82	22.20± 2.88	5.22± 1.35	- -	- -	- -
March	5	76.82±12.38	7.26± 3.28	1.38± 0.56	- -	14.62±10.25	- -
April	6	43.84± 8.28	23.78± 6.75	9.87± 2.12	2.a.± 1.48	20.85± 5.59	- -
May	6	36.28±10.81	8.67± 3.78	9.97± 2.68	8.23± 0.23	45.45± 9.88	- -
June	6	8.43± 4.56	10.87± 3.19	5.28± 1.92	0.43± 0.43	75.37± 4.96	- -
July	6	8.28± 3.96	14.15± 5.13	7.83± 3.87	17.58± 5.48	53.83±13.99	- -
August	8	4.56± 2.12	23.99± 7.69	4.84± 1.28	32.19± 6.41	34.34±10.61	- -

Appendix 4.

Species of Forbs Encountered but Not Seen to be Eaten during the Recording Sessions.

i. Kudus

Acalypha peticlaris
Acanthosicyos naudiniana
Achyranthes sicula
Antherious cooperi
Antizoma harveyana
Asclepias fruticosa
Asparagus saunderiae
Barleria scabra
Bulbine angustifolia
Cleome maculata
Corchorus kirkii
Crotilaria pisicarpa
Cyanotis speciosa
Cryptolepis oblongifolia
Dicerocaryum zanguebarium
Dicoma macrocephala
Dipcardi viride
Euphorbia inaequilatera
Felicia muricata
Gomphrena celosioides
Helichrysum krausii
Hibiscus subreniformis
Indigofera daleoides
Jatropha zeyheri
Kalenchoe paniculata
Kohautia virgata
Ledebouria graminifolia
Limium fenestratum
Melhania prostrata
Monchoma divaricatum
Nidorella resedifolia
Oxalis corniculata
Parinari capensis
Parvetta zeyheri
Pellaea calomelanos
Pentarrhinum insipidum
Phyllanthus parvulus
Polygala sphenoptera
Portulaca quadrifida
Pterocactus africana
Rhoicissus tridentata
Rhynchosia confusa
Rhynchosia venulosa
Sida rhomboidifolia
Tagetes minuta
Tribulus terrestris
Trochomeria macrocarpa
Turbina oblongata
Vernonia staehelinoides

Plus 18 unidentified species encountered only once or twice.

Appendix 4.

Species of Forbs Encountered but Not Seen to be Eaten during the Recording Sessions.

ii. Impala

Acalypha petiolaris

Achyrospis leptostachya

Aloe davyana

Amaranthus thunbergii

Anthericum galpinii

Antizoma harveyana

Asclepias burchelli

Asclepias fruticosa

Asparagus saunderiae

Bauhinia macrantha

Bidens bipinnata

Blepharis maderaspatensis

Boophane disticha

Borreria scabra

Bulbine angustifolia

Cassia absus

Cerotothecs triloba

Cleome maculata

Commeline benghalensis

Commelina ecklonians

Commelina livingstonei

Conyza floribunda

Corchorus kirkii

Crotilaria pisicarpa

Cyanotis speciose

Cypnocarpa angustifolia

Dicoma macrocephala

Dipcardi marlothii

Dipcardi viride

Euphorbia inaequilatera

Fadogia monticola

Gladeolus cf. calcartus

Hemizygia canescens

Hemizygia petrensis

Hypoxis obtusa

Indigofera comosa

Indigofera distincha

Indigofera filipes

Indigofera nebrowniana

Indigofera sordida

Indigofera viciodes

Ipomea ommaneyi

Justicia anagalloides

Kalanchoe paniculata

Kohautia virgata

Ledebouria graminifolia

Leucas neuflizeana

Linsum fenestratum

Linsum viscosum

Lophiocarpus tenuissimus

Melhania prostrata

Nidorella resedifolia

Ocimum canum

Opuntia ficus-indica

Oxalis corniculata

Oxygonium dregeanum

Oxygonium sinatum

Phyllanthus maderaspatensis

Raptionacm burkei

Rhynchosia confusa

Rhynchosia longiflora

Rhynchosia monophylla

Rhynchosia rinenosa

Ruellia cordata

Ruellia malacophylla

Ruellia patula

Continued. . .

Schkuhria pinnata	Tagetes minuta
Senecio inaequidens	Talinum caffrum
Senicio longifolia	Tephrosia longipes
Senecio venosus	Thunbergia neglecta
Sida alba	Tribulus terrestris
Sida hoepfneri	Triumfetta pentondra
Sida pseudofolia	Triumfetta sonderi
Solanum seaforthianum	Vernonia fastigiata
Sphedamnocarpus pruriens	Vernonia monocephala
Striga asiatica	Vernonia poskeana
Striga gesnerioides	Xerophyta retinervis
Stylocanthes fruticosa	Zinnia multiflora
Subera burkeana	Zornia capensis

Plus 55 unidentified species encountered only once or twice.

Appendix 4.

Species of Forbs Encountered but Not Seen to be Eaten during the Recording Sessions.

iii. Goats

Agathisanthemum bojeri

Aloe davyana

Amaranthus deflexus

Anthericum galpinii

Asparagus saundersiae

Brayulinea densa

Cassia absus

Commelina benghalensis

Commelina eckloniana

Corchorus kirkii

Crotilaria sphaerocarpa

Cyanotis speciosa

Cyphocarpa angustifolia

Dicerocaryum zanguebarium

Elephantorrhiza obliqua

Euphorbia inaequilatera

Fadogia monticola

Gomphrena celosioides

Hemizygia petrensis

Hermannia boraginiflora

Hibiscus hesusei

Hibiscus subreniformis

Indigofera comosa

Indigofera distincha

Indigofera nebrowniana

Indigofera sordida

Jatropha zeyheri

Justicia anagalloides

Justicia spergulaefolia

Limeum fenestratum

Ocimum canum

Opuntia ficus-indica

Oxalis corniculata

Parinari capensis

Pavonia transvaalensis

Pellaea colomelanus

Plumbago zeylanica

Polygala sphenoptera

Raphionacme burkei

Rhynchosia densiflora

Ruellia cordata

Salecia reinnanii

Schkuhria pinnata

Sida cryasantha

Sida hospinsi

Sida ovata

Sida pseudofolia

Stylocanthes fruticosa

Tagetes minuta

Tephrosia longipes

Tephrosia lupinifolia

Thesium cytisoides

Thunbergia neglecta

Vernonia fastigiata

Vernonia poskeana

Vernonia staehelinoides

Xerophyta retinervis

Zinnia multiflora

Plus 22 unidentified species encountered only once or twice.

Appendix 5.

Availability Leaves and Twigs of Woody Plant Species Within Reach of Browsers (under 2.5 m)

Species	%	Species	%
Acacia nilotica	2.8	Ehretia rigida	Rare
Acacia tortilis	3.1	Erythrococca menyharthii	0.05
Burkea africana	11.3	Euclea crispa	Rare
Combretum molle	0.3	Euclea undulata	0.05
Dichrostachys cinerea	2.8	Gardenia spatulifolia	0.05
Dombeya cotundifolia	1.7	Grewia bicolor	0.1
Euclea natalensis	0.05	Grewia flava	0.05
Grewia flavescens	14.8	Grewia monticola	0.2
Ochna pulchra	55.0	Lannea discolor	0.05
Peltophorum africanum	0.2	Lannea edulis	Rare
Rhus leptodictya	0.2	Maytenus tenuispina	0.1
Strychnos pungens	0.5	Mundulea sericea	0.05
Terminalia sericea	3.8	Ozoroa paniculosa	0.05
Vitex rehmannii	0.8	Pappea capensis	Rare
Acacia burkei	Rare	Protea welwitschii	Rare
Acacia caffra	Rare	Pseudolachnostylis	Rare
Acacia hebeclada	Rare	maprounifolia	Rare
Acacia kacoo	0.1	Pygmaeothamnus zeyheri	Rare
Barleria bremekampii	Rare	Rhus pyroides	Rare
Bequertiodendron magalismontanum	Rare	Sclerocarya caffra	Rare
Bridelia mollis	Rare	Securidaca longipedunculata	0.2
Canthium gilfillanii	Rare	Securinega virosa	Rare
Carissa bispinosa	Rare	Strychnos cocculoides	0.3
Cassine transvaalensis	Rare	Strychnos madagascariensis	Rare
Combretum apiculatum	Rare	Tarchonanthus camphoratus	Rare
Combretum zeyheri	1.3	Vitex nombassae	Rare
Croton gratissimus	Rare	Vangueria infaustra	Rare
Dichapetalum cymosum	Rare	Ximenia caffra	0.05
Diospyros lycioides	0.05	Ziziphus mucronata	0.1

Appendix 6.

A Comparison of the Concentrations of Total Polyphenols Measured in the Mature Leaves of Woody Plants by the Jerumanis and Folin-Denis Methods

Method	Jerumanis			Folin-Denis		
Species	Mean	SE	n	Mean	SE	n
Acacia nilotica	28.1	+ -	1	17.4	+ Ø.2	5
Acacia tortilis	8.5	+ -	1	7.8	+ Ø.1	5
Burkea africana	1Ø.4	+ -	1	11.8	+ Ø.5	6
Combretum molle	17.6	+ -	1	12.3	+ Ø.5	5
Dichrostachys cinerea	15.8	+ -	1	14.3	+ Ø.3	4
Peltophorum africanum	15.6	+ -	1	14.4	+ Ø.4	5

Appendix 7.

The Effect of Different Drying Techniques and Solvents on the Measurement of Condensed Tannin (Proanthocyanidin)

Drying	Air Dried			Freeze Dried			Freeze Dried		
Solvent	*Acetone*			*Acetone*			*Methanol*		
Species	Mean	SE	n	Mean	SE	n	Mean	SE	n
Acacia nilotica	0.0	± 0.0	8	0.0	± 0.0	6	0.0	± 0.0	5
Acacia tortilis	3.0	± 0.2	8	4.8	± 0.2	7	2.8	± 0.2	5
Burkea africana	5.8	± 0.9	6	10.3	± 0.7	7	6.3	± 0.5	5
Combretum molle	1.0	± 0.1	8	0.8	± 0.1	8	0.5	± 0.1	5
Dichrostachys cinerea	3.5	± 0.2	8	8.3	± 0.6	8	5.8	± 0.8	5

Appendix 8.

Plant Secondary Compounds Reported for Plant Species in the Study Area

(From Watt & Breyer-Brandwijk 1962)

Plant Species	Compound	Action
i. Alkaloids		
Asclepias spp.	Nicotine	Mild poisoning
Zinnia spp.	Nicotine	
Crotilaria spp.	Pyrrolizidine alkaloid	"Crotilariosis"
Cotyledon spp.	Cotyledontoxin	Neuromuscular toxin
Kalanchoe spp.	Cotyledontoxin	"Cotyledonosis"
Senecio spp.	Senecifoline, Senecifolidine	Anti-mitotic
Solanum spp.	Solanine, Solanidine	
Lantana rugosa	Lantanin	Non-toxic
ii. Cyanogenic glycosides		
Tephrosia spp.		
Acacia tortilis		
Commelina benghalensis		
Dichapetalum cymosum		
Mundulea sericea		
Tribulus terrestris		
iii. Terpenes		
Labiate spp.	Monoterpenes	
Clerodendron spp.	Diterpenes	
Lantana spp.	Diterpenes	Non-toxic
Euphorbiaceae	Diterpenes	Irritant latex
Cucurbitaceae	Triterpene cucurbitans	Respiratory paralysis, gastrointestinal irritation
Elephantorrhiza spp.	Steroids	
Carissa bispinosa	Steroids	
Vangueria infaustra	Steroids	
Waltheria indica	Steroids	

Appendix 8 continued. . .

iv. Saponins

Aloe spp.		Haemolytic
Carissa bispinosa		

v. Cardiac glycosides

Carissa spp		
Asclepias fruticosa		Heart toxin

vi. Toxic glucosides

Terminalia sericea	Nerifolin	

vii. Strychnine

Strychnos cocculoides (seeds)		

viii. Oxalates

Opuntia spp.	Calcium oxalate	Scouring
Oxalis spp.	Calcium oxalate	Mineral imbalance
Portulaca quadrifida	Potassium oxalate	Mineral imbalance

ix. Monofluoroacetate

Dichapetalum cymosum	Heart toxin	Interferes with the pyruvate metabolism causing accumulation of citric acid

x. Polyphenols

Aloe spp.	Astringent
Bidens spp.	
Combretum spp.	
Crassula spp.	Mildly astringent
Euclea spp.	Non-astringent
Acacia karoo	
Acacia nilotica	
Carissa bispinosa	
Waltheria indica	

xi. Mucilage

Dicerocaryum zanguebarium

xi. Other toxins

Hermannia tomentosa		Mild toxin
Ochna pulchra (new leaves)		Mild toxin
Nidorella resedifolia	Alkaloid?	"Staggers"

Appendix 9

MULTIVARIATE STATISTICS

Information on plant species acceptance by browsing ungulates and concentrations of chemical compounds in the leaves of woody plants and in whole forbs was subjected to multivariate analysis using SAS statistical packages.

Initially a stepwise discriminant analysis (STEPDISC), using forwards and backwards selection was used to determine the order of significance of chemical factors. The full range of chemical measures was in excess of the number permitted for the limited number of species observations in the data set. Hence the chemical measures were split into two groups. Nutrients plus moisture and fibre plus digestion reducing compounds.

Discriminant function analysis was used to distinguish between favoured and non-preferred plant species on the basis of the chemistry of the mature, green leaves.

The plants were classified into two a priori groups. 'Preferred' plants were those of consistently high acceptance, or of moderate acceptance in the growing season but eaten increasingly in the early dry season. 'Non-preferred' plants were those of consistently low acceptance or species only eaten at certain times of year such as O. pulchra eaten only when in new

Appendix 9 continued. . .

leaf and E. natalensis eaten in the late dry season when the availability of browse was at a minimum.

Canonical discriminant function analysis (CANDISC) is a dimension-reducing technique related to principal components analysis. This technique was used to identify the linear concentration of chemical measures that best summarised the differences among the favoured and non-preferred groups of plants. This was followed by the DISCRIM procedure which placed each species into the preference group from which it has the smallest generalised squared distance, and identified which species, if any, were misclassified by the chemical measures selected by canonical discriminant function analysis.

Principal components analysis (FACTOR) is a multivariate technique for examining relationships between several uncorrelated quantitative variables and detects linear relationships between variables. Each principal component is a linear combination of the original variables with coefficients equal to the eigenvectors of the correlation matrix. The first principal component has the largest variance of any linear combination of variables. Subsequent principal components have the largest variance of any linear combinations orthogonal to the previous axis. Principal components analysis was used to determine which chemical measures accounted for the greatest variance within the plant species with no a priori classification being imposed on the data.

The chemical measures were tested for skewness and kurtosis by

Appendix 9 continued. . .

the MEANS procedure and found to be of normal distribution. Standardisation of the data to remove effects of units of measure was achieved through the use of correlation matrices rather than covariance matrices in the analysis.

Appendix 10

Checklist of the Browse Plants Occurring within the Enclosure for the Tame Animals at Nylsvley

POLYPODIACEAE

Pellaea calomelanus.

COMMELINACEAE

Commelina africana L.

Commelina benghalensis L.

Commelina eckloniana Kunth.

Commelina erecta L. var. livingstonei (C.B.Cl.) A.Morton.

Cyanotis speciosa (L.f.) Hassk.

LILIACEAE

Bulbine angustifolia V. Peolin.

Anthericum cooperi Bak.

Anthericum galpinii Bak. var. galpinii

Aloe davyana Schonl. var. davyana.

Dipcadi viride (L.) Moench.

Ledebouria graminifolia Bak.

Asparagus africanus Lam.

Asparagus buchananii Bak.

Asparagus saunderiae Bak.

Asparagus suaveolens Burch.

Appendix 10 continued. . .

AMARYLLIDACEAE

Boophane disticha (L.f.) Herb.

HYPOXIDACEAE

Hypoxis obusta Burch ex Edwards.

VELLOZIACEAE

Xerophyta retinervis Bak.

IRIDACEAE

Gladiolus cf. calcaratus Lewis.

PROTEACEAE

Faurea saligna Harv.

Protea cf. welwitschii Engl.

SANTALACEAE

Thesium cytisoides A.W.Hill.

OLACACEAE

Ximenia caffra Sond. var. caffra.

POLYGONACEAE

Oxygonum dregeanum Meisn.

Oxygonum sinuatum (Hochst. & Steud. ex Meisn.) Damm.

CHENOPODIACEAE

Chenopodium album (L.).

Appendix 10 continued. . .

AMARANTHACEAE

Hermbstaedtia odorata (Burch) T.Coohe.

Amaranthus thunbergii Moq.

Amaranthus deflexus L.

Cyphocarpa angustifolia Lopr.

Achyranthes aspera L.

Achyranthes leptostachya Hook.

Achyranthes sicula (L.) All.

Achyropsis leptostachya (E.May ex Meisn) Hook.F.

Gomphrena celosioides Mart.

Brayulinea densa (Willd.) Small.

AIZOACEAE

Limeum fenestratum (Fenzl) Heimerl.

Limeum viscosum (Gay) Fenzl subsp. viscosum.

PORTULACACEAE

Talinum caffrum (Thunb.) Eckl. & Zeyh.

Portulaca quadrifida L.

Portulaca pilosa L.

CARYOPHYLLACEAE

Pollichia campestris Soland. in Ait.

Antizoma harveyana Miers. ex Harv.

CAPPARIDACEAE

Cleome maculata (Sond.) Szyszyl.

Appendix 10 continued. . .

CRASSULACEAE

Kalanchoe paniculata Harv.

Kalanchoe rotundifolia Harv.

ROSACEAE

Parinari capensis Harv.

LEGUMINOSAE

subfam. MIMOSOIDEAE (MIMOSACEAE)

Acacia burkei Benth.

Acacia caffra (Thunb.) Willd.

Acacia hebeclada D.C.

Acacia karroo Hayne.

Acacia nilotica (L.) Willd. ex Del. subsp. kraussiana (Benth.) Brenan.

Acacia tortilis (Forsk. Hayne subsp. heteracantha (Burch.) Brenan.

Dichrostachys cinerea (L.) Wight & Arn.

Elephantorrhiza obliqua Burtt Davy var. glabra Phill.

subfam. CAESALPINIOIDEAE (CAESALPINIACEAE)

Burkea africana Hook.

Bauhinia macrantha Oliv.

Cassia abus L.

Cassia capensis Thunb. var. capensis.

Peltophorum africanum Sond.

Appendix 10 continued. . .

subfam. PAPILIONOIDEAE (FABACEAE)

Lotononis calycina (E.Mey) Benth var. hirsutissima Duemmer.

Crotalaria pisicarpa Welw.

Crotalaria sphaerocarpa Perr. ex DC.

Indigofera comosa N.E.Br.

Indigofera cf.daleoides Benth.

Indigofera distincha Eckl. & Zeyh.

Indigofera filipes Benth.

Indigofera macra E. Mey.

Indigofera nebrowniana Gillett.

Indigofera sordida Benth.

Indigofera vicioides Juab & Spach.

Tephrosia forbesii Bak.

Tephrosia longipes Meisn.

Tephrosia cf. lupinifolia (Burch.) DC.

Mundulea sericea (Willd.) A.Chev.

Stylosanthes fruticosa (Retz.) Alston.

Zornia capensis Pers.

Rhynchosia confusa Burtt Davy.

Rhynchosia densiflora (Roth) D.C.

Rhynchosia longiflora Schinz.

Rhynchosia monophylla Schltr.

Rhynchosia venulosa (Hievn.) K.Schim.

OXALIDACEAE

Oxalis corniculata (L.)

Appendix 10 continued. . .

ZYGOPHYLLACEAE

Tribulus terrestris L.

MALPIGHIACEAE

Sphedamnocarpus pruriens (Juss.) Szyszyl.

POLYGALACEAE

Polygala sphenoptera Fresen.

Securidaca longipedunculata Fresen.

DICHAPETALACEAE

Dichapetalum cymosum (Hook.) Engl. & Prantl.

EUPHORBIACEAE

Pseudolachnostylis maprouneifolia Pax.

Securinega virosa (Roxb. ex Willd.) Pax & Hoffm.

Phyllanthus maderaspatensis L.

Phyllanthus parvulus Sond.

Phyllanthus pentandrus K. Schum. & Thonn.

Bridelia mollis Hutch.

Croton gratissimus Burch. var. *subgratissimus* (Prain) Burtt Davy.

Erythrococca menyharthii (Pax) Prain.

Acalypha petiolaris Hochst.

Pterococcus africana (Sond.) Pax & Hoffm.

Jatropha zeyheri Sond.

Euphorbia inaequilatera Sond.

Appendix 1Ø continued. . .

ANACARDIACEAE

Sclerocarya caffra Sond.

Lannea discolor (Sond.) Engl.

Lannea edulis (Sond.) Engl.

Ozoroa paniculosa (Sond.) R. & A. Fernandes.

Rhus dentata Thunb.

Rhus leptodictya Diels.

Rhus cf. pyroides Burch.

CELASTRACEAE

Maytenus heterophylla (Eckl. & Zeyh.) N.Robson.

Maytenus tenuispina (Sond.) Marais.

Cassine transvaalensis (Burtt Davy) Codd.

Salacia rehmannii Schinz.

SAPINDACEAE

Pappea capensis (Spreng.) Eckl. & Zeyh.

RHAMNACEAE

Ziziphus mucronata Willd.

VITACEAE

Rhoicissus tridentata (L.f.) Wild & Drumm.

Cyphostemma puberulum (C.A.Sm) Wild & Drumm.

TILIACEAE

Corchorus kirkii N.E.Br.

Grewia bicolor Juss.

Appendix 10 continued. . .

Grewia flava DC.

Grewia flavescens Juss. var. Flavescens.

Grewia monticola Sond.

Triumfetta pentandra A.Rick.

Triumfetta rhomboidea Jacq.

Triumfetta sonderi Fical. & Hiern.

MALVACEAE

Sida alba L.

Sida chrysantha Ulbr.

Sida cordifolia L.

Sida hoepfneri Guerke.

Sida ovata Forsk.

Sida rhombifolia L.

Sida pseudocordifolia Hochr.

Pavonia transvaalensis (Ulbr.) A. Meeuse.

Hibiscus engleri K. Schum.

Hibiscus subreniformis Burtt Davy.

Hibiscus meeusei Exell.

STERCULIACEAE

Melhania prostrata DC.

Dombeya rotundifolia (Hochst.) Planch.

Hermannia boraginiflora Hook.

Hermannia grisea Schinz.

Hermannia quartiniana A. Rich.

Hermannia tomentosa (Turcz.) Schinz ex Engl.

Waltheria cf. indica L.

Appendix 10 continued. . .

OCHNACEAE

Ochna pretoriensis Phill.

Ochna pulchra Hook.F.

CACTACEAE

Opuntia ficus-indica Mill.

COMBRETACEAE

Combretum apiculatum Sond.

Combretum molle R.Br. ex G.Don.

Combretum zeyheri Sond.

Terminalia sericea Burch.ex DC.

PLUMBAGINACEAE

Plumbago zeylanica L.

SAPOTACEAE

Bequaertiodendron magalismontanum (Sond.) Heine & Hemsl.

EBENACEAE

Euclea crispa (Thunb.) Guerke var. crispa.

Euclea natalensis A.DC.

Euclea undulata Thunb.

Diospyros lycioides Desf. subsp. lycioides.

LOGANIACEAE

Strychnos cocculoides Bak.

Appendix 10 continued. . .

Strychnos madagascariensis Poir.

Strychnos pungens Soler.

APOCYNACEAE

Carissa bispinosa (L.) Desf. ex Brenan.

PERIPLOCACEAE

Cryptolepis oblongifolia Schltr.

Raphionacme burkei N.E.Br.

ASCLEPIADACEAE

Asclepias burchellii Schltr.

Asclepias cf. fruticosa L.

Pentarrhinum insipidum E.Mey.

CONVOLVULACEAE

Evolvulus alsinoides (L.) L. var. linifolius (L.) Bak.

Merremia tridentata subsp. angustifolia (Jacq.) Ooststr.

Ipomoea obscura (L.) Ker-Gawl. var. fragilis (Choisy) A.Meeuse.

Ipomoea ommaneyi Rendle.

Turbina oblongala (E.Mey ex Choisay.) E.Meeuse.

BORAGINACEAE

Ehretia rigida (Thunb.) Druce.

VERBENACEAE

Lantana rugosa Thunb.

Lippia javanica (Burm.f.) Spreng.

Appendix 10 continued. . .

Vitex mombassae Corb.

Vitex rehmannii Guerke.

Clerodendrum caeruleum N. H.Br.

Clerodendrum ternatum Schinz.

LABIATAE

Leucas neuflizeana Courb.

Hemizygia canescens (Guerke) M.Ashby.

Hemizygia petrensis (Hiern) Ashby.

Ocimum canum Sims.

Ocimum ureticifolium Roth.

Becium angustifolium (Benth.) N.E.Br.

SOLANACEAE

Solanum coccineum Jacq.

Solanum incanum L.

Solanum panduraeforme E.Mey.

Solanum saeforthianum Andr.

SCROPHULARIACEAE

Sutera burkeana Hiern.

Striga asiatica (L.) Kuntze.

Striga gesnerioides (Willd.) Vatke.

PEDALIACEAE

Dicerocaryum zanguebarium (Lour.) Merrill.

Ceratotheca triloba E.Mey.

Appendix 10 continued. . .

ACANTHACEAE

Thunbergia atriplicifolia E.Mey.

Thunbergia neglecta Sond. subsp. neglecta.

Chaetacanthus costatus Nees.

Ruellia cordata Thunb.

Ruellia malacophylla C.B.Cl.

Ruellia patula Jacq.

Crabbea hirsuta Harv.

Barleria bremekampii Oberm.

Blepheris maderaspatensis L.F.Heyne ex Roth.

Justicia anagalloides T.Anders.

Justicia flava (Vahl) Vahl.

Justicia incerta C.B.Cl.

Justicia minima A.Meeuse.

Justicia spergulaefolia T.Anders.

Monechma divaricatum (Nees) C.B.Cl.

RUBIACEAE

Agathisanthemum bojeri Klotzsh.

Kohautia virgata (Willd.) Brem.

Oldenlandia herbacea (L.) Roxb.

Gardenia spatulifolia Stapf & Hutch.

Vangueria infausta Burch.

Pygmaeothamnus zeyheri (Sond.) Robyns.

Canthium gilfillanii (N.E.Br.) Miller.

Fadogea monticola Robyns.

Pavetta zeyheri Sond.

Borreria scabra (Schumach. & Thonn.) K.Schum.

Appendix 10 continued. . .

CUCURBITACEAE

Acanthosicyos naudiniana (Sond.) Jeffrey.

Cucumis heptadactylus Naud.

Trochomeria macrocarpa (Sond.) Hook.f.

ASTERACEAE

Vernonia fastigiata Oliv. & Hiern.

Vernonia oligocephala (DC.) Sch. Bip; ex Walp.

Vernonia poskeana Vatke & Hildebr.

Vernonia staehelinoides Harv.

Felicia fascicularis DC.

Felicia mossamedensis (Hiern) Mendonca.

Felicia muricata (Thunb.) Nees subsp. muricata.

Nidorella resedifolia DC.

Conyza floribunda H.B.K.

Tarchonanthus camphoratus L.

Helichrysum candelleanum Buek.

Helichrysum kraussii Sch. Bip.

Zinnia multiflora L.

Zinia peruviana (L.) L.

Bidens bipinnata L.

Bidens pilosa L.

Schkuhria pinnata (Lam.) Kuntze ex Thell.

Senecio inaequidens DC.

Senecio longifolia D.C.

Senecia venosus Harv.

Dicoma anomala Sond.

Appendix 1Ø continued. . .

Dicoma macrocephala DC.

Tagetes minuta L.

Callilepis leptophylla Harv.