Resistance of leaf and stem fractions of tropical forage to chewing and passage in cattle

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(*Received 20 March 1989 – Accepted 28 August 1989*)

The voluntary intake (VI) of separated leaf and stem fractions of a grass and legume (*Panicum maximum* and *Lablab purpureus* respectively) was determined using Hereford steers fistulated at the rumen and oesophagus. VI of leaf fractions was higher than that of the stem fraction (8·23 *v.* 3·67 kg/d, $P < 0·001$) while that for the legume diets was higher than for the grass diets (6·65 *v.* 5·22 kg/d, $P < 0·05$). The total number of eating chews per day was higher on the leaf than stem fraction ($1·6 \times 10^4$ *v.* $9·8 \times 10^3$, $P < 0·05$). The mean number of rumination chews ($2·4 \times 10^4$) was similar ($P > 0·05$) for all four diets. The mean resistance of large particles (LP, i.e. retained on a 1·18 mm sieve during wet sieving) to breakdown (chews per g LP breakdown) during eating was lower for leaf than stem fractions (8·4 *v.* 23·7) and lower for the grass than legume diets (10·5 *v.* 21·6). The mean resistance to breakdown of LP by rumination (chews per g LP breakdown) was lower in leaf than in stem fractions (8·2 *v.* 13·2, $P < 0·01$) and higher in grass than in legume (12·5 *v.* 9·0, $P < 0·05$). The resistance of LP to breakdown during rumination was higher than during eating for the grass diets, but was lower for the legume. Fractional passage rates (FPR) of small particles (i.e. passing through a 1·18 mm sieve during wet sieving) from the reticulo-rumen were negatively related to dimensions of particles, with greater ease of outflow for legume than for grass particles of the same length or diameter. When corrected for content of cellulase-indigestible fibre, FPR of small particles of leaf was greater than for small stem particles. It was concluded that VI of tropical forages was associated with the resistance of LP to breakdown by chewing during both eating and rumination and that the patterns of escape of small particles from the reticulo-rumen were only partially explicable in terms of particle dimensions, and that other properties of the particles may be of importance.

Chewing resistance: Digesta passage: Ruminant digestion

Voluntary feed intake (VI) of low-quality dried herbages is considered to be limited by the 'fill' of dry matter (DM) and its low clearance from the reticulo-rumen (Bines, 1971; Weston & Kennedy, 1984). Before digesta can pass into the abomasum of cattle, most of the particles must be reduced below a critical size, suggested by Poppi *et al.* (1985) to be described by particles able to pass a screen of 1·18 mm pore size during wet sieving. Most of this reduction in size is achieved by chewing during eating and rumination with only 17% of the reduction attributable to digestion and detrition (McLeod & Minson, 1988). Therefore, resistance to breakdown of forage large particles (LP) could be a major factor controlling the rate of passage of digesta from the rumen and hence the VI of forages. In addition, as the rate of passage of small particles (SP) from the reticulo-rumen is negatively related to particle size (Poppi *et al.* 1985), the size spectrum of the SP derived from LP breakdown might be expected to influence the rate of digesta passage from the reticulo-rumen. In this context it has been suggested that both size and functional specific gravity

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of particles modulate the movement of particles within the reticulo-rumen (Sutherland, 1988).

The relative importance of LP breakdown and SP passage has been discussed (Poppi *et al.* 1981*c*) but direct experimental assessment has been rendered difficult by interactions between these factors resulting from integration of the function of the reticulo-rumen by the animal. For instance, when the requirement for LP breakdown is removed by grinding and pelleting of forages, reduction in chewing effort may reduce passage or increase it by reducing entrapment of SP in the 'raft' of buoyant particles in the dorsal rumen (Sutherland, 1988) leading to unpredictable effects on passage and fill (Weston & Kennedy, 1984). These effects of chewing behaviour indicate that chewing and associated LP breakdown may be more significant in the control of VI than indicated by the relative content or retention times of LP and SP in the reticulo-rumen.

The present paper describes a study using leaf and stem preparations of a grass and a legume, which produce large differences in VI (Minson, 1982), designed to measure resistance of LP breakdown during eating and rumination, and rates of passage from the reticulo-rumen of SP of different sizes. Tropical forages with a high-fibre content were used to ensure that VI was limited by physical characteristics of the diet and not by the rate at which cattle could utilize energy.

EXPERIMENTAL

Diets and animals

Pure swards of the grass, Green panic (*Panicum maximum* var. *trichoglume*) and the legume, Lablab (*Lablab purpureus* cv. Rongai), were cut after 3 months growth, chopped to 20–40 mm lengths, dried at 100° and separated into a 'leaf' and 'stem' fraction using a gravity seed separator (Laredo & Minson, 1973). The purity of the fractions was determined by hand separation into leaf lamina, leaf sheath and true stem. The petiole of Lablab was included in the stem fraction. Samples of the four diets were analysed for neutral-detergent fibre (NDF) (ash-free; Van Soest & Wine, 1967), acid-detergent fibre (ADF) (ash-free; Van Soest & Wine, 1967) and lignin (ash-free; Van Soest, 1963), and nitrogen, phosphorus, calcium, sulphur, potassium, sodium, boron, copper, manganese and zinc by emission spectroscopy (Johnson & Simons, 1972). Other constituents of the plant were estimated as follows: hemicellulose = NDF (ash-free) − ADF (ash-free); cellulose = ADF (ash-free, following NDF extraction) − lignin (ash-free); neutral-detergent-soluble organic matter (NDSOM) = 100 − (NDF + feed ash).

The four feeds were offered *ad lib.* during four periods of 15 d with 7 d adaptation in a Latin-square design to four Hereford steers fistulated at the rumen and oesophagus and weighing between 349 and 455 kg (mean 385 kg). Feeds were offered at hourly intervals to the four steers and VI and digestibility measured as previously described (Poppi *et al.* 1981*a*). The total number of chews and the number of eating chews were recorded by separate digital impulse counters, which were connected to a device consisting of a microswitch attached to a halter with a cable under the jaw for detecting movement (Stobbs & Cowper, 1972). A mercury switch, positioned to allow current to flow when the animal's head is in the eating position, permitted jaw movements to be recorded separately during eating. The number of rumination chews was calculated as the difference between the two readings. At the end of each period, the reticulo-rumen contents were removed through the fistula, weighed, mixed thoroughly and subsampled for particle analysis.

LP breakdown

The breakdown of LP during primary mastication was determined by measuring the proportion of LP in the diet and in the material swallowed after chewing. The swallowed material was collected via the oesophageal fistula.

The particle spectrum (by weight) of the four diets and oesophageal extrusa was determined by the wet-sieving method developed for soil analysis (Bourget & Kemp, 1957). The method was modified for use with forages by collecting the very small particles that passed through the bottom 0·15 mm screen ('fines'). Forage (10 g) was soaked overnight and wet sieved using a nest of six sieves (pore sizes 4·76, 2·41, 1·18, 0·50, 0·31 and 0·15 mm) suspended in a tank of water and oscillated through a vertical distance of 65 mm at a frequency of 40 strokes/min for 10 min. The particle retained on each sieve were dried and weighed. Fines were estimated on a portion of the water remaining in the tank after adjusting the volume to 40 litres. The fine particles were allowed to settle overnight, the supernatant fraction removed and the particles transferred to a tared dish, dried and weighed. The particle weight distribution in the sample was calculated as percentage (by weight) of the total weight of particles (including fines) present. Total particle DM determined in this way was water-extracted DM. LP were defined as those particles which were retained on the top three sieves (4·75, 2·36 and 1·18 mm; Poppi *et al.* 1985) and SP as those passing the 1·18 mm sieve. Particles passing through a sieve with an aperture of 0·50 mm but retained on the sieve with an aperture of 0·30 mm were described as $> 0{\cdot}30$ particles and those passing the 0·15 mm screen as $< 0{\cdot}15$ particles. Dimensions (length and diameter) of twenty particles, selected at random from each of the sieved fractions for each animal, were measured with a Nikon profile projector. Only solitary particles, free of aggregates or debris, were measured.

Reticulum motility and rumination

Biphasic contractions of the reticulum were measured over 6 h using a pressure transducer attached to an open-ended catheter located in the reticulum.

Marker studies

Markers of the fluid phase (CoNaEDTA) and a chromium-labelled SP fraction (Cr-SP) of rumen digesta were prepared as described by Udén *et al.* (1980). The Cr labelled particles were prepared from Green panic and Lablab stem ground through a 1 mm screen, suspended in a nylon bag (50 μm pore size) for 72 h in the rumen, and subsequently extracted with neutral-detergent solution (Van Soest & Wine, 1967). After labelling with Cr, the distributions of particles after wet sieving on screens of aperture 0·50, 0·30, 0·15 mm and those passing the 0·15 mm sieve, were 3·9, 31·2, 31·4 and 33·4% for Green panic and 20·2, 53·0, 20·7 and 6·1% for Lablab. All fractions collected contained 120–157 g Cr/kg DM.

Markers (4 g Co as CoNaEDTA in 100 ml, 25 g Cr-SP) were dosed into the rumen. Samples of rumen fluid and digesta were taken at 4, 8, 12, 28 and 32 h after dosing. To reduce variability due to inadequate sampling of SP and LP fractions, the LP were removed by manually sieving digesta (10 g DM) plus water (2 litres) successively through sieves of aperture 11·5, 4·0 and 2·0 mm. The resultant suspension was centrifuged (15 min, 1100 ***g***), the supernatant fraction decanted, and the SP fraction was dried (100°) before analysing for Cr. Co and Cr were determined by atomic absorption spectrophotometry after dilution for Co, and by the procedure described by Williams *et al.* (1962) for Cr.

Potential digestibility

Cellulase (*EC* 3.2.1.4)-insoluble fibre was used as an internal indigestible marker to correct for post-ruminal digestion of SP. After wet sieving, particles were recovered from the sieves, dried and ground through a screen of 1 mm aperture. Following extraction with neutral detergent, particle fractions were incubated with Onozuka FA cellulase (6 g/l; extracted from *Trichoderma viride*; Maruzen Chemical Co. Ltd, Osaka, Japan) in acetate buffer (McLeod & Minson, 1978) for 12 d at 50°, with the cellulase–buffer solution being

replaced daily. After drying, residues were subjected to acid detergent (Van Soest, 1963), dried, and finally combusted at 550° for 3 h. Feed samples (ground through a 1 mm screen) were likewise subjected to cellulase digestion over 12 d.

Calculations

The quantity of LP broken down during primary mastication (eating) was estimated from DM intake and the difference in proportion of LP in the feed offered and in the sample of swallowed feed collected from the oesophageal fistula. The quantity of LP broken down by secondary mastication (rumination) was estimated from the LP swallowed minus the quantity of particles excreted in the faeces. When calculated in this way no allowance is made for the LP broken down by digestion and detrition. The loss in weight of particles between feed and faeces was estimated from the increase in lignin content using the following equation:

$$\text{feed particle DM (g)} = \frac{\text{faecal particle DM (g)} \times \text{faecal lignin (g/kg DM)}}{\text{feed lignin (g/kg DM)}}.$$

The resistance of LP to breakdown was expressed as the number of chews required to convert 1 g LP into small particles and was calculated as follows:

$$\text{resistance of LP to breakdown} = \frac{\text{number of chews (per d)}}{\text{LP broken down (g/d)}}.$$

Apparent mean retention times (h) of DM and particulate DM in the rumen (i.e. not corrected for digestion) were calculated by dividing the rumen pool by the mean hourly consumption during the previous 48 h (Minson, 1966). Fractional passage rates (FPR,/d) of NDF in SP fractions were derived by dividing faecal output (g/d) by the rumen pool (g) after correcting for digestion distal to the rumen using cellulase-insoluble fibre as an internal indigestible marker. FPR from the rumen of markers of fluid and SP were calculated as the slope of the $\log_e$ concentration of marker *v.* time.

Statistics

The significance of differences between feeds, animals and periods was assessed by analysis of variance for a Latin square design and orthogonal comparisons were made between grass *v.* legume, leaf *v.* stem, and their interaction (Steel & Torrie, 1980)

RESULTS

Composition of the diets

The physical characteristics of the four diets are shown in Table 1. The leaf and stem fractions produced by gravity separation were 75–86% leaf and 98–99% stem. The leaf fractions contained both lamina and sheath, while the stem fractions contained some leaf sheath and lamina in addition to true stem. The LP content of the leaf fractions was lower than that of the stem fractions, probably because the leaf LP were more prone to shattering during drying and separation into fractions. This was particularly evident with the legume leaf fraction.

The stem fractions contained more fibre constituents and less neutral-detergent-solubles than did the leaf fractions (Table 1). Fibre (NDF, ADF) concentrations were lower in the legume fractions than in the corresponding grass fractions. Hemicellulose (NDF − ADF) concentrations were higher in the grass fractions than in the legume, with the levels in leaf being only slightly higher than those in the stem fraction. Cellulose concentrations

Table 1. *Physical characteristics and chemical composition of the four contrasting diets*

	Grass (*Panicum maximum*)		Legume (*Lablab purpureus*)	
	Leaf	Stem	Leaf	Stem
Physical characteristics				
Proportion of leaf	0·85	0·01	0·75	0·02
Proportion of stem	0·15	0·99	0·25	0·98
Total particles (g/kg DM*)	770	790	760	800
Large particles† (g/kg DM)	698	748	582	745
Organic composition (g/kg DM)				
NDSOM	172	137	418	268
NDF (ash-free)	683	751	456	610
ADF (ash-free)	369	470	277	455
Hemicellulose	314	288	179	156
Cellulose	324	402	224	369
Lignin	45	67	58	86
Macroelements (g/kg DM)				
Ash	147	112	124	124
Nitrogen	17·3	10·8	37·0	16·5
Phosphorus	2·4	1·9	4·0	4·1
Calcium	5·9	2·5	22·7	13·9
Sulphur	1·9	1·3	2·6	2·0
Potassium	18·3	20·4	24·0	40·4
Sodium	11·3	12·0	0·1	0·1
Trace elements (mg/kg DM)				
Boron	11	< 1	79	36
Copper	13	9	11	12
Manganese	86	50	98	41
Zinc	47	43	50	50

DM, dry matter; NDSOM, neutral-detergent-soluble organic matter; NDF, neutral-detergent fibre; ADF, acid-detergent fibre.

* Water-extracted DM.

† Those particles retained on the top three sieves (4·75, 2·36 and 1·18 mm; Poppi *et al.* 1985).

(ADF − lignin) were higher in the grass fractions than in the corresponding legume fractions. Lignin levels were higher in the legume fractions than in the corresponding grass fractions.

Although there were no significant differences between the four feeds in ash content, the P, Ca, S and K contents were higher in the legume fractions than in the corresponding grass fractions, while Na was very much lower in the legume. None of these differences should have affected the VI of these forages.

VI and DM digestibility

Cattle ate more leaf than stem with both forages ($P < 0·001$) and more legume than grass ($P < 0·05$, Table 2). No significant differences in DM digestibilities were evident between grass and legume, but the stem was more digestible ($P < 0·05$) than the leaf fraction with both forages.

Mastication

The total number of chews each day was the same for the grass and legume diets ($3·63 \times 10^4$ and $3·76 \times 10^4$; $P > 0·05$, Table 2). Cattle tended to chew more when fed on the leaf than

Table 2. *Mean voluntary intake, chewing behaviour, breakdown of large particles (LP) and rumen characteristics of cattle fed on four contrasting diets containing leaf and stem fractions of two tropical forages*

Forage species...	Grass (*Panicum maximum*)		Legume (*Lablab purpureus*)			Orthogonal contrasts		
Fraction	Leaf	Stem	Leaf	Stem	SEM (6 df)	Grass *v.* legume	Leaf *v.* stem	Interaction
Dry matter (DM) intake								
kg/d	7·18	3·27	9·27	4·03	0·348†	*	***	—
g/kg body-wt per d	18·7	8·5	23·9	10·5	0·74	**	***	—
Digestible DM intake (kg/d)	3·65	1·94	4·74	2·20	0·153	**	***	*
Digestibility of DM	0·510	0·587	0·514	0·546	0·0205	—	*	*
Number of chews ($\times 10^4$)								
Primary mastication	1·65	0·93	1·55	1·03	0·184	—	*	—
Secondary mastication	2·28	2·39	2·52	2·43	0·166	—	—	—
Chews (/g DM intake)	5·46	10·09	4·38	8·62	0·816	—	**	—
LP (kg/d)								
Eaten	5·01	2·44	5·39	3·00	0·188†	*	***	—
Entering rumen	2·78	1·76	3·74	2·70	0·128†	***	***	—
Excreted in faeces‡	0·14	0·17	0·31	0·26	0·029	**	—	—
Broken down by primary and secondary mastication §	4·86	2·28	5·08	2·74	0·199†	—	***	—
Proportion of LP broken down by								
Primary mastication	0·45	0·28	0·31	0·10	0·018	***	***	—
Secondary mastication	0·54	0·70	0·68	0·89	0·021	***	***	—

Resistance to breakdown (chews/g LP broken down)								
Primary mastication	7·41	13·62	9·41	33·88	1·029	***	***	—
Rumination	9·07	15·87	7·40	10·57	0·987	*	**	—
All mastication	8·09	14·60	8·01	12·59	0·992	*	**	—
Rumen content of								
DM (kg)	7·48	5·05	7·41	6·38	0·435	—	***	**
Particulate DM (kg)	6·08	4·20	6·10	5·31	0·389	—	*	—
LP (kg)	2·00	1·54	2·17	2·71	0·251	*	—	—
Fluid (kg)	59·9	46·7	47·7	58·1	3·85	—	—	**
Apparent retention time in rumen (h)								
DM	23·9	33·4	17·3	35·6	1·42	—	***	*
Particulate DM	25·7	37·8	22·4	40·7	2·55	—	**	—
LP	16·7	18·6	12·0	22·7	2·6	—	**	—
Reticular motility (contractions/h)	69·5	65·0	65·4	61·8	2·81	—	**	—
Rumination time (min/d)	425	423	468	460	31·8	—	—	—
Rumen fluid passage ‖								
l/h	8·64	4·39	7·78	4·56	0·559	—	***	—
ml/contraction	113	67	119	73	2·8	*	***	—
Faecal fines/rumination (g/min)	2·19	0·65	2·77	0·67	0·230	—	***	**

DM, dry matter.
* $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.
† Significant between-animal effects ($P < 0·05$).
‡ Corrected for loss in weight using a lignin ratio technique.
§ Ignoring LP broken down by digestion and detrition.
‖ Calculated from rumen fluid volume obtained by emptying × turnover rate of CoEDTA.

the stem fraction ($4{\cdot}00 \times 10^4$ *v.* $3{\cdot}39 \times 10^4$/d, Table 2). This difference was caused by a difference in the number of primary mastication chews (leaf, $1{\cdot}6 \times 10^4$ chews/d; stem, $9{\cdot}8 \times 10^3$ chews/d; $P < 0{\cdot}05$) and was associated with a greater intake of leaf than of stem. Rumination (secondary mastication) chews were not affected by diet, and averaged $2{\cdot}4 \times 10^4$ chews/d. The number of chews per unit DM intake varied from 4·4 to 10·1 chews/g with the leaf fractions requiring less chewing than the stem ($P < 0{\cdot}01$).

Breakdown of LP

Quantities of LP eaten, entering the rumen, and excreted in the faeces were greater for the legume diet ($P < 0{\cdot}05$, Table 2). More leaf LP were eaten and entered the rumen than stem LP but there was no corresponding difference in faecal LP excretion ($P < 0{\cdot}001$, Table 2).

Mastication, during eating and rumination, reduced between 2·3 and 5·1 kg LP in the forage to SP each day (Table 2). The quantity of LP broken down was higher with leaf than with stem (4·97 *v.* 2·51 kg/d, $P < 0{\cdot}001$) and was directly related to higher intake of the leaf fraction. The quantity of LP broken down to SP was similar for the grass and legume (3·57 *v.* 3·91 kg/d). Primary mastication caused the breakdown of 38% of the LP in the leaf fraction compared with 19% in the stem fraction ($P < 0{\cdot}001$). The LP in both fractions of the grass were broken down more during primary mastication than LP in the corresponding legume fractions ($P < 0{\cdot}001$).

Resistance of LP to breakdown during primary mastication was lower for the leaf than stem fraction (8·4 *v.* 23·8 chews/g, $P < 0{\cdot}001$). The LP in the grass fraction had a lower resistance to breakdown during primary mastication than the LP in the legume (10·5 *v.* 21·6 chews/g, $P < 0{\cdot}001$). During rumination the mean resistance to breakdown of LP was higher for grass than for legume (12·5 *v.* 9·0 chews/g LP, $P < 0{\cdot}05$) and higher for stem than for leaf diets (13·2 *v.* 8·2 chews/g LP, $P < 0{\cdot}01$). On rumination, the LP in the regurgitated digesta of the grass fractions were more resistant to breakdown than were the LP in the original forage that were broken down during primary mastication, but the opposite applied to the legume.

The quantity of rumen LP was higher ($P < 0{\cdot}05$) in animals fed on legume, but was similar ($P > 0{\cdot}05$) for the leaf and stem fractions. The reverse situation applied for the quantity of total rumen particles.

Rumen fill and flow

Rumen pools of DM and particulate DM, were greater ($P < 0{\cdot}05$) when the animals were fed on leaf than when fed on stem (Table 2). Feeding of leaf instead of stem increased rumen fluid pools for grass, but reduced them for legume (interaction $P < 0{\cdot}01$). Apparent retention times of DM and forage particles in the rumen were approximately 65% higher ($P < 0{\cdot}01$) for stem diets than leaf diets and this was related to a 44% lower VI of the stem fraction. The movement of the greater quantity of leaf DM and SP through the rumen was associated with a higher reticular contraction rate ($P < 0{\cdot}01$). Fluid flow from the rumen (l/h and ml/reticular contraction) was also higher for leaf diets ($P < 0{\cdot}001$). Fluid flow from the rumen (l/h or ml/contraction) was correlated with VI (kg DM/d) according to the relationships:

$$\text{Fluid flow (l/h)} = 2{\cdot}02 + 0{\cdot}729\ \text{VI} \qquad (1)$$

(residual standard deviation (RSD) 1·43, r^2 0·66, $P < 0{\cdot}001$).

$$\text{Fluid flow (ml/contraction)} = 39{\cdot}4 + 9{\cdot}04\ \text{VI} \qquad (2)$$

(RSD 11·7, r^2 0·82, $P < 0{\cdot}001$).

FPR of liquid (NaCoEDTA) and particulate (Cr-SP) markers were higher ($P < 0{\cdot}01$) for leaf than for stem fractions but were unaffected ($P > 0{\cdot}05$) by plant species (Table 3).

Table 3. *Fractional passage rates of particle fractions (internal marker basis) and of markers of the fluid (CoEDTA) and particle (Cr-SP)† phases of rumen digesta, and digestion of particles by cellulase (EC 3.2.1.4) in cattle fed on four contrasting diets containing leaf and stem fractions of two tropical forages*

(Particle fractions are described in the form > 0·30: particles in this fraction are retained on the sieve of 0·30 mm pore size and pass through the previous sieve of 0·50 mm pore size. Fractional passage rates and post-rumen digestion are expressed on a neutral-detergent fibre basis)

Forage species...	Grass (*Panicum maximum*)		Legume (*Lablab purpureus*)			Orthogonal contrasts		
Particle fraction	Leaf	Stem	Leaf	Stem	SEM	Grass *v.* legume	Leaf *v.* stem	Interaction
			Fractional passage rate (/d)					
> 0·50 mm	0·280	0·149	0·553	0·416	0·0116	**	*	—
> 0·30 mm	0·700	0·459	1·010	1·010	0·0530	**	—	—
> 0·15 mm	1·625	0·627	1·022	1·022	0·2348	—	*	—
> 0·15 + > 0·30 + > 0·50 mm	0·676	0·384	0·627	0·627	0·0218	*	*	—
			Marker fractional passage rate (/d)					
CoEDTA	3·63	2·49	3·94	1·88	0·375	—	**	—
Cr-SP	1·03	0·87	1·48	0·87	0·102	—	**	*
			Relative post-rumen change in digestion (%)					
> 0·50 mm	39·5	39·5	35·0	23·9	1·21	**	—	—
> 0·30 mm	37·7	33·5	25·0	33·8	5·42	—	—	—
> 0·15 mm	27·2	18·9	26·2	36·9	0·80	—	—	*

* $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.
† Chromium-labelled small particle fraction.

Apparent FPR for rumen particle fractions, not corrected for internal marker content, are shown in Fig. 1(*a*). Higher rates for legume than for grass diets ($P < 0·01$) were observed for > 1·18, > 0·50 and > 0·30 particles. When apparent FPR was related to measured dimensions of particles, it was clear that, on average, legume particles moved from the reticulo-rumen or were digested in the caecum, or both, with greater ease than grass particles. Also, leaf particles tended to flow faster than stem particles at a given particle length or diameter (Fig. 1(*b*, *c*)).

When FPR of NDF in particles was corrected for post-rumen digestion by reference to an internal marker (cellulase-insoluble fibre), significant differences were found in FPR of the > 0·05, > 0·30 and > 0·15 particles with the following trends being evident (Table 3): (a) FPR tended to be negatively related to particle size; (b) FPR for legume diets was greater than for grass diets for > 0·50 and > 0·30 particles, but not for > 0·15 particles; (c) the absolute difference between FPR of leaf compared with stem diets increased with decreasing particle size, with the principle effect attributed to the steers fed on Green panic. The FPR of (> 0·15 + > 0·30 + > 0·50) particles was greater for Lablab than for Green panic ($P < 0·05$) and for leaf than for stem fractions ($P < 0·05$). These differences were largely due to the low FPR of Green panic stem.

Correction for content of cellulase-insoluble fibre increased FPR by 9, 8 and 8% respectively for > 0·50, > 0·30 and > 0·15 particles when compared with calculations on an uncorrected basis. The bias introduced by not correcting for the internal marker was somewhat variable; FPR across the three particle groups calculated by reference to

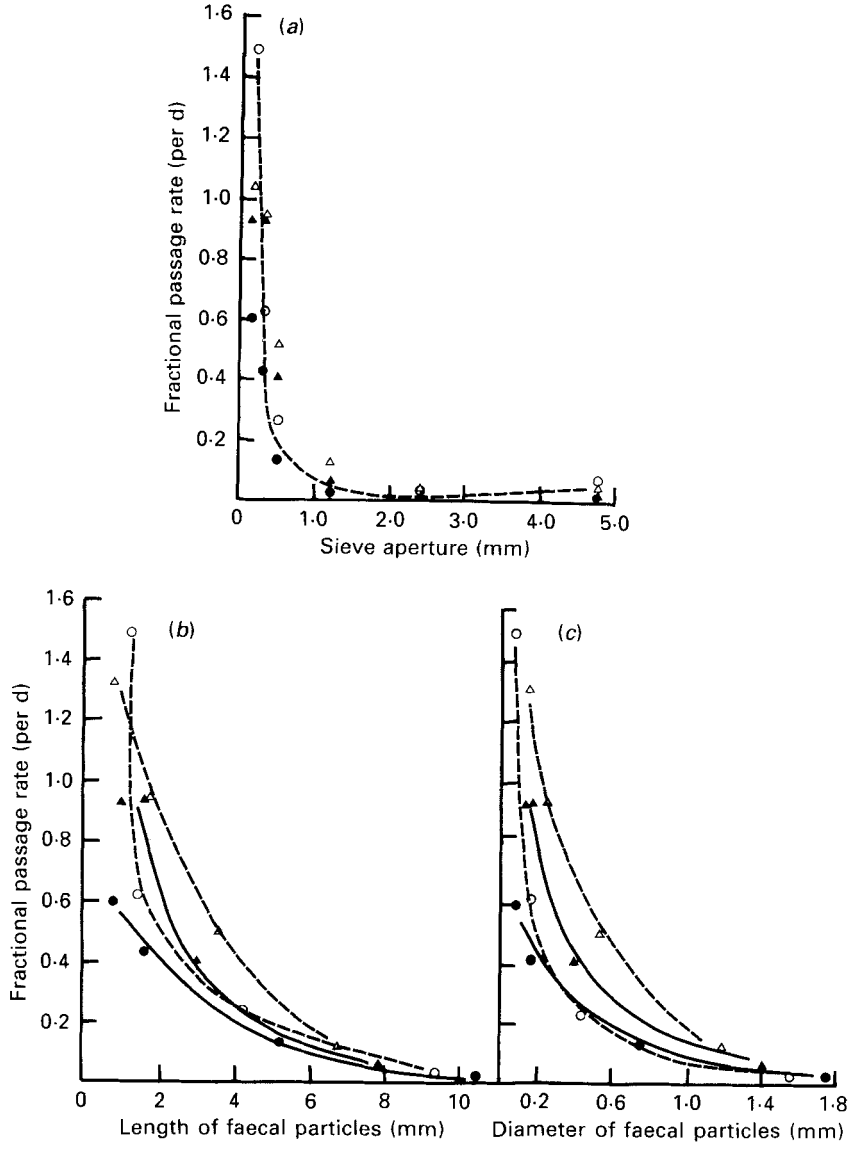

Fig. 1. Relationship of apparent passage outflow rate (not corrected for internal marker) of particles retained on sieves *v.* (*a*) screen aperture of sieves, (*b*) mean length and (*c*) mean diameter of particles. Grass (*Panicum maximum*) leaf (○), stem (●); legume (*Lablab purpureus*) leaf (△), stem (▲).

cellulase-insoluble fibre exceeded apparent FPR by 13, 6, 9 and 7% for grass leaf and stem and legume leaf and stem respectively.

Mean length (mm) of faecal particles was related to mean length (mm) of rumen particles retained on sieves of pore size 0·15, 0·31, 0·50, 1·18 and 2·41 mm as follows:

Green panic leaf and stem

$$\text{faecal length} = 0{\cdot}126 + 0{\cdot}931 \text{ rumen length} \quad (3)$$

(RSD 1·25, r^2 0·91, $P < 0{\cdot}001$).

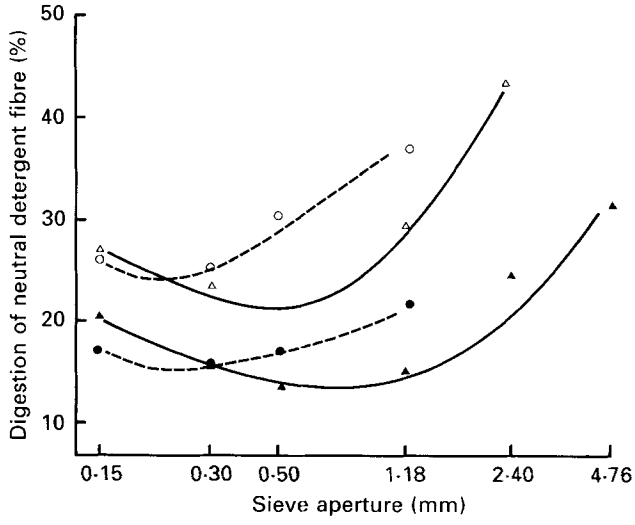

Fig. 2. Digestion by cellulase (*EC* 3.2.1.4) of neutral-detergent fibre (NDF) in sieved particles of rumen digesta as a function of screen aperture of sieves on which particles are retained. Grass (*Panicum maximum*) leaf (○), stem (●); legume (*Lablab purpureus*) leaf (△), stem (▲).

Lablab leaf and stem

$$\text{faecal length} = 0{\cdot}729 + 0{\cdot}566 \text{ rumen length} \quad (4)$$
(RSD 0·435, r^2 0·98, $P < 0{\cdot}001$).

Digestion of NDF by cellulase in rumen particles occurred to a substantially greater extent ($P < 0{\cdot}001$) in leaf than in stem diets. Within diets, the extent of cellulase digestion of particle fractions from rumen digesta decreased with decreasing screen sizes to a minimum for > 0·31 (Green panic) and 0·50 (Lablab) and thereafter increased for smaller particles (Fig. 2). Digestion by cellulase over 12 d removed 42, 27, 48 and 33% of the NDF in Green panic leaf and stem, and Lablab leaf and stem fractions, respectively.

Fine (< 0·15) particles comprised more (33 *v.* 21%, $P < 0{\cdot}001$) faecal particulate matter in animals fed on leaf than in those fed on stem. Appearance of fine particles in the faeces per min of rumination was greater in leaf than in stem fractions and greater in Lablab leaf than for Green panic diets (Table 2).

Relations with VI

The VI of the four contrasting feeds was negatively related to the number of chews required per g DM (Fig. 3), with a lower number of chews for the leaf fraction than for the stem fraction. The higher intake of the leaf fraction appeared to be associated with the lower resistance of the LP fraction to breakdown during both primary and secondary mastication (Table 2).

Voluntary intake of the four diets were also positively related to rates of passage of markers of the fluid ($P < 0{\cdot}01$) and SP ($P < 0{\cdot}05$) fractions. In addition VI (kg/d) of stem diets was related to DM in the reticulo-rumen as follows:

$$\text{VI} = 0{\cdot}909 + 0{\cdot}480 \text{ rumen DM pool} \quad (5)$$
(RSD 0·191, r^2 0·96, $P < 0{\cdot}001$).

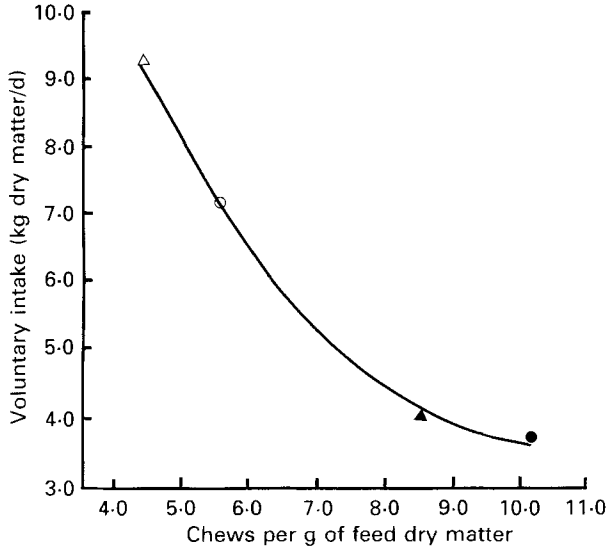

Fig. 3. Relation between voluntary intake (y) and the number of eating and ruminating chews required per unit of feed (x). Grass (*Panicum maximum*) leaf (○), stem (●); legume (*Lablab purpureus*) leaf (△), stem (▲).

Regression: $y = 20{\cdot}2 - 3{\cdot}2\,x + 0{\cdot}15\,x^2$, n 4, r 0·99, SE of the estimate 0·22.

DISCUSSION

Breakdown of LP appears to be required before a particle may be cleared from the reticulo-rumen (Poppi *et al.* 1985) and the present study has indicated the importance of chewing in the clearance of contrasting forages with very different chemical and morphological properties, as shown by the relationship of VI to the resistance of forage to breakdown during chewing (Fig. 3). The higher VI of the leaf than the stem fraction of both the grass and legume was associated with a lower proportion of LP in the leaf fraction, a greater number of primary chews and lower resistance of the leaf LP to breakdown to SP during primary mastication. The combined effect led to three to five times more leaf than stem LP being broken down by primary mastication. The intake of the leaf fraction was further enhanced by the high level of neutral-detergent-soluble organic matter and the smaller proportion of LP (Table 1).

The number of ruminating chews each day was similar for all four feeds and was not a factor contributing to the higher intake of the leaf fraction. However, the resistance to breakdown of LP in the leaf fraction regurgitated during rumination was again lower than that of the stem fraction indicating greater fragility. The size distribution of SP in the rumen and in the faeces also suggested that the greater fragility of leaf diets resulted in finer particles.

The VI of legume leaf was 29% higher than that of grass leaf. This appears to be only partially explained by the lower intake of LP in the legume (4·23 kg) than in the grass leaf (4·90 kg), due to the lower content of cell wall material in the legume (Table 1). The higher VI of the stem fraction of the legume appears to be associated with a low resistance to breakdown during rumination.

SP resulting from chewing, digestion and detrition of the forage are retained in the

reticulo-rumen for various lengths of time before passing through the reticulo-omasal orifice. To what extent VI is limited by the rate of passage of those SP from the reticulo-rumen has not been established but it is known that there are only small differences in VI of contrasting forages once the LP are removed by grinding and pelleting (Heaney *et al.* 1963). The differences in rate of passage of fluid and SP in the present study provides some evidence of the effect of VI of forage on rumen variables. The positive association of fluid flow from the reticulo-rumen and VI observed in the present experiment is in agreement with previous studies using similar diets (Hendricksen *et al.* 1981; Poppi *et al.* 1981*b*), although the quantity of fluid flowing per kg DM intake was higher in the present experiments. The higher flow in cattle given leaf was attributed mainly to the larger quantity of SP that left the rumen and a higher fluid passage per reticular contraction, although the latter appears to be less important.

A significant finding from the present work is that rates of passage of particles of the same length or diameter varied markedly between diets (Fig. 1(*b*, *c*)). The results in Fig. 1(*b*, *c*) also confirm the finding of Dixon & Milligan (1985), Egan & Doyle (1985) and Poppi *et al.* (1985), among others, that ease of particle flow is proportional to particle size. The faster passage of legume compared with grass has been ascribed to differences in particle shape (Troelsen & Campbell, 1968), but may also reflect higher functional specific gravity or lower buoyancy of legume particles. In the study of Hooper & Welch (1985), values (1·2–1·4; Welch, 1986) of specific gravity conducive to rapid passage were achieved more rapidly in legumes than in grasses, perhaps due to the presence of fewer hydrophobic molecules in legume cell walls (see Gates *et al.* 1987). In the present experiment, the relationship between faecal and rumen particle lengths collected on the same sieves during wet sieving differed markedly between grass and legume diets (Eqns (3) and (4)). As the wet-sieving process is influenced by specific gravity as well as dimensions of particles, this result is suggestive of a greater change in functional specific gravity for Lablab particles while passing through the gastrointestinal tract, perhaps due to selection for passage from the reticulum of less buoyant particles.

Further differences between the legume and grass diets were evident in patterns of cellulase-available NDF (Fig. 2). The content of cellulase-available NDF in $> 0{\cdot}15$ particles of leaf and stem fractions of legume was equivalent to that of material from sieves of theoretical aperture 1·0 and 2·3 mm respectively, whereas for $> 0{\cdot}15$ particles of grass leaf and stem, the theoretical sieves had apertures of 0·35 and 0·51 mm. We postulate that these differences, which were associated with lower resistance to breakdown of legume LP during rumination (Table 2), suggest more extensive fragmentation of legume LP to $> 0{\cdot}15$ particles than for grass LP, and for relatively greater selection for passage of extensively digested $> 0{\cdot}15$ legume particles, with those remaining in the rumen being relatively buoyant and digestible.

The above discussion has highlighted differences in LP breakdown observed in contrasting forages of high-fibre content requiring prolonged rumination (7 h/d). If chewing assists in the passage of SP through effects on 'raft' reduction and accelerated passage of SP from the reticulum, as well as its requirement for LP breakdown, then the calculated value of 'resistance to LP breakdown' during chewing appears useful in the prediction of VI. Future validation of the use of 'resistance to LP breakdown to chewing' in prediction of VI would suggest that laboratory measurements of forage fragility of good predictive power could be achieved. Such a technique would require criteria of particle size which could be related to those found in ruminants.

It is concluded that VI of tropical forages was associated with the resistance of LP to breakdown to SP by chewing during both eating and rumination, and that the patterns of

escape of particles from the reticulo-rumen were only partially explicable in terms of particle dimensions, and that other properties of the particles may be of importance. The role of plant anatomy in the resistance of forages to breakdown during chewing and the presence of specialized structures which affect microbial digestion remain to be resolved.

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Printed in Great Britain