

## Forage and splanchnic tissue mass in growing lambs: effects of dietary forage levels and source on splanchnic tissue mass in growing lambs

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Forty-two crossbred lambs (33.4 kg initial body weight; twenty-four wethers and eighteen ewes) were used in a 42 d experiment with a 2 × 3 factorial treatment arrangement to determine effects of forage level and source on splanchnic tissue mass. Diets were 250 and 750 g/kg of chopped lucerne (*Medicago sativa*) (A), ryegrass (*Lolium multiflorum*)–wheat (*Triticum aestivum*) (RW) or bermudagrass (*Cynodon dactylon*) (B) hay, with the remainder being maize-based concentrate. Five lambs per treatment were slaughtered at the end of the experiment and measurements made of internal organs and contents of the gastrointestinal tract (GIT). Digestible organic matter intake (DOMI) on the 7 d preceding slaughter was 0.89, 0.83, 0.90, 0.83, 0.77 and 0.61 (SE 0.05) kg/d, and live-weight gain was 0.20, 0.17, 0.18, 0.10, 0.10 and 0.07 (SE 0.02) kg/d for diets A-25, RW-25, B-25, A-75, RW-75 and B-75 respectively. Total GIT mass (fresh) was higher ( $P < 0.05$ ) for 750 than 250 g forage/kg and for B than RW (4.80, 4.57, 5.55, 5.84, 5.99 and 6.91 kg for diets A-25, RW-25, B-25, A-75, RW-75 and B-75 respectively). Non-fat organic matter was 259, 295, 292, 303, 277 and 264 g for the total GIT; 93, 102, 103, 106, 95 and 97 g for the reticulo-rumen (forage level × type (diet A *v.* diets RW and B) interaction;  $P < 0.05$ ); and 204, 196, 202, 177, 156 and 127 g for the liver (SE 10) with diets A-25, RW-25, B-25, A-75, RW-75 and B-75 respectively. In summary, differences in properties of forage A and the grasses at 250 g/kg diet may have influenced GIT mass independent of energy intake and digesta mass. Conversely, with 750 g dietary forage/kg, higher digesta mass for diet B than diet RW appeared responsible for high reticulo-rumen mass relative to DOMI. Greater digesta mass for 750 than 250 g forage/kg may have elevated intestinal tissue mass/DOMI with diets A and B but not with diet RW, for which NDF digestibility was highest.

### Splanchnic tissue mass: Forage: Lambs

Splanchnic tissues consume much energy and amino acids relative to their proportions of the whole body (Webster, 1980; Ferrell, 1988). Energy use by splanchnic tissues relates to organ mass (Ferrell *et al.* 1986; Johnson *et al.* 1990) and rises with increasing energy intake because of increasing demands for service functions of precursor organs and greater use of energy in cell maintenance functions such as integrity of ion gradients and protein turnover (McBride & Milligan, 1984; Ferrell, 1988). Generally, the absorptive workload rather than the quantity or characteristics of digesta in the small intestine is thought to have a major impact on small intestinal mass and energy consumption (Johnson *et al.* 1990). However, Bailey (1986) suggested that digesta weight, texture or chemical composition affect GIT mass. In support, an inert substance added to diets of lambs increased weight of the stomach complex and/or large intestine (Rompala *et al.* 1988, 1990). Likewise, as a proportion of empty-body weight (EBW), total GIT mass for Holstein steers from 100 kg

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to over 400 kg was greater with high-forage diets than for high-concentrate diets (Bailey, 1986). Conversely, Johnson (1988) concluded that fermentable fibres stimulate GIT tissue growth whereas inert fibres do not. Forages differ considerably in the quantity and nature of fibre. Legumes typically contain less cell walls than grasses, and temperate grasses are less fibrous than tropical grasses (Minson, 1990). Legume cell walls are high in lignin, being degraded less extensively but more rapidly than grass cell walls (Mertens & Loftén, 1980). Tropical grass cell walls normally are higher in lignin (Jung & Fahey, 1983; Windham *et al.* 1987) and are digested more slowly and less completely than cell walls of temperate grass (Mertens & Loftén, 1980). Therefore, the present experiment was conducted to determine effects and interactions of dietary forage level (250 and 750 g/kg) and source (legume *v.* grasses and temperate *v.* tropical grass) on splanchnic tissue mass in growing lambs.

## MATERIALS AND METHODS

### *Animals and diets*

Forty-two lambs ((Rambouillet  $\times$  Dorset)  $\times$  Hampshire; twenty-four wethers and eighteen ewes), approximately 3.5 months of age and obtained from one source, were shorn, dewormed and housed individually in an enclosed building with free access to water. For a 14 d pre-experimental period the lambs were fed on a limited amount of ground maize and consumed bermudagrass (*Cynodon dactylon*) hay *ad lib*. Then, lambs were weighed full (without feed restriction) at 06.00 hours on days -1, 0, 20, 21, 41 and 42 of the experiment. Lambs were allotted to six treatments based on body weight on day -1 and sex for similar mean body weight and variation in body weight within treatment and sex (four wethers and three ewes/treatment). Average initial body weight (mean of day -1 and 0) was 33 (SE 0.3) kg.

The treatment design was a 2  $\times$  3 factorial with two levels of forage and three forage sources. Diets consisted of 250 or 750 g/kg lucerne (*Medicago sativa*; vegetative; A), ryegrass (*Lolium multiflorum*; early head emergence)-wheat (*Triticum aestivum*; anthesis; RW) or bermudagrass (*Cynodon dactylon*; early heading; B) hay, and the remainder was concentrate consisting predominantly of ground maize. All hay was chopped to pass a 19 mm screen. Composition of diets, forage and concentrate is shown in Tables 1 and 2. Diets were formulated to be isonitrogenous, dietary proportions of N from supplemental protein sources were standardized, and concentrate was in meal form. Treatments were designated as A-25, RW-25, B-25, A-75, RW-75 and B-75, with 25 and 75 referring to the level of dietary forage. Diets were offered once daily at 15.00 hours at 105 to 110% of consumption on previous days. Orts were weighed immediately before feeding. Hay and concentrate supplements were weighed separately, mixed by hand before feeding, and sampled daily to form weekly composites. Composites were ground through a 1 mm screen and analysed for dry matter (DM), ash, Kjeldahl N (Association of Official Analytical Chemists, 1984), neutral-detergent fibre (NDF; Goering & Van Soest, 1970; without decalin or sodium sulphite) and acid-detergent fibre and lignin (ADL; Goering & Van Soest, 1970).  $\alpha$ -Amylase (EC 3.2.1.1) was used in supplement NDF analysis (Cherney *et al.* 1989). Average daily body-weight gain and gain:feed (DM) were calculated using average body weight on consecutive days.

### *Slaughter measurements*

Thirty lambs (three wethers and two ewes/treatment) were slaughtered and eviscerated at the end of the experiment over a 3 d period. One wether and one ewe from each treatment were slaughtered on the first 2 d, and one wether from each treatment was slaughtered on the third day. Organs were immediately tied at junctions, separated and weighed. Gastrointestinal tract components were the reticulo-rumen, omasum, abomasum, small

Table 1. *Composition of diets (g/kg dry matter) fed to lambs*

Diet* ...	A-25	RW-25	B-25	A-75	RW-75	B-75
Ingredient						
Lucerne ( <i>Medicago sativa</i> ) hay (A)	250.0	—	—	750.0	—	—
Ryegrass ( <i>Lolium multiflorum</i> )-wheat hay (RW)	—	250.0	—	—	750.0	—
Bermudagrass ( <i>Cynodon dactylon</i> ) hay (B)	—	—	250.0	—	—	750.0
Ground maize	656.9	627.6	630.1	221.3	155.4	163.5
Blood meal	12.0	14.8	14.8	2.4	10.8	10.6
Soya-bean meal	39.5	49.9	49.7	8.0	36.1	35.5
Feather meal	11.9	15.0	14.9	2.4	10.9	10.7
Maize-gluten meal	16.2	19.9	19.8	3.2	14.5	14.2
Trace mineral premix†	0.5	0.5	0.5	0.5	0.5	0.5
Dicalcium phosphate	2.0	2.5	3.0	4.7	5.5	6.6
Salt	2.0	2.0	2.0	2.0	2.0	2.0
Vitamin premix‡	0.3	0.3	0.3	0.3	0.3	0.3
Bovatec®	0.2	0.2	0.2	0.2	0.2	0.2
Limestone	3.5	12.3	9.7	—	8.8	0.9
Soya-bean oil	5.0	5.0	5.0	5.0	5.0	5.0
Composition						
Ash	37	38	39	65	73	76
N	28.6	27.0	26.6	29.1	26.1	26.1
Neutral-detergent fibre	208	227	263	408	478	580

\* Dietary forage (A, RW or B) was included at 250 or 750 g/kg diet.

† Contained (g/kg) air-dry premix: Ca 70–80, Zn  $\geq$  120, Fe 100, Mn 80, K 50, Mg 25, Cu 15, Co 3, Se 0.2.

‡ Contained (mg/kg) air-dry premix: vitamin A 600, cholecalciferol 10, vitamin E 230.

intestine, caecum and large intestine. Other tissues included the liver, heart, lungs, spleen, kidneys, and visceral fat. Digesta were removed from GIT segments, and empty tissue and digesta mass were determined. The reticulo-rumen, omasum, abomasum, caecum and large intestine were washed with tap water, and residual water was removed. EBW was determined by subtracting digesta mass from full-body weight measured immediately before slaughter. Small intestinal length was measured as well; organs were frozen after measurements. After partial thawing at room temperature, tissues were chopped, subsampled, lyophilized and reweighed. Subsamples were ground in a household coffee mill and analysed for DM, ash and diethyl ether extract (Association of Official Analytical Chemists, 1984). Ash was quantified with a muffle furnace (600° for 6 h).

#### Digestion

For 14–17 d before slaughter, Cr<sub>2</sub>O<sub>3</sub> was fed at 1.5 g/kg diet by being thoroughly mixed with concentrate. All digesta in the large intestine were collected at slaughter, lyophilized and ground to pass a 1 mm screen. Samples of diets, orts (7 d before slaughter) and large intestinal digesta were analysed for DM, ash, NDF, N and Cr (Williams *et al.* 1962). Cr was determined by atomic absorption spectroscopy with an acetylene plus N<sub>2</sub>O flame, and used as an external marker to estimate total tract digestibility.

#### Statistical analysis

Data were analysed with dietary treatment, sex and the treatment  $\times$  sex interaction in the statistical model. Sex was retained when its effect was significant ( $P < 0.05$ ); the interaction was not significant and dropped from all analyses. Orthogonal contrasts were conducted for effects of forage level, forage type (legume *v.* grasses), grass type, forage level  $\times$  forage

Table 2. *Composition (g/kg dry matter) of lucerne (Medicago sativa; A), ryegrass (Lolium multiflorum)–wheat (Triticum aestivum; RW), bermudagrass (Cynodon dactylon; B) and concentrate fed to lambs*

	Forage			Concentrate*					
	A	RW	B	A-25	A-75	RW-25	RW-75	B-25	B-75
Ash	71	78	81	25	46	24	58	25	60
N	31	21	21	28	25	29	43	29	43
Neutral-detergent fibre	500	594	732	111	130	104	128	107	124
Acid-detergent fibre	361	316	329	47	51	40	55	45	61
Acid-detergent lignin	80	34	58						
Cellulose	264	257	254						
Hemicellulose	139	278	403						

\* Dietary forage (A, RW or B) was included at 250 or 750 g/kg; for details of composition, see Table 1.

Table 3. *Intake, digestibility, performance and slaughter measurements for lambs fed on diets of 250 or 750 g lucerne (Medicago sativa; A), ryegrass (Lolium multiflorum)–wheat (Triticum aestivum; RW) or bermudagrass (Cynodon dactylon; B) hay/kg\**

Forage level (L; g/kg)...	250			750			SE	Statistical analysis: effects were significant ( $P < 0.05$ ) for:
	A	RW	B	A	RW	B		
Dietary forage...								
Dry matter intake (kg/d)†	1.17	1.13	1.13	1.12	1.11	0.90	0.059	L
Digestibility (%)‡								
Organic matter	75.4	78.7	77.4	69.9	71.3	64.8	1.17	L, G, L × F, L × G
Neutral-detergent fibre	40.5	51.5	49.3	60.1	69.6	62.0	1.75	L, F, G
N	68.5	66.9	69.4	67.5	63.1	66.5	1.36	L, G
Live-wt gain (kg/d)†	0.20	0.17	0.18	0.10	0.10	0.07	0.024	L
Gain:feed dry matter†	0.17	0.15	0.16	0.09	0.09	0.07	0.017	L
Live wt at slaughter (kg)‡								
Full (unshrunk)	43.3	41.2	42.8	39.0	40.3	37.1	1.52	L
Empty	38.5	36.6	37.2	33.2	34.3	30.2	1.24	L
Carcass wt (kg)‡	20.9	19.9	20.4	17.5	18.2	16.9	0.60	L
<i>Longissimus muscle</i> ‡								
Fat depth (mm)	8.3	4.4	6.1	3.9	5.7	3.7	0.79	L, L × F, L × G
Area (mm <sup>2</sup> )	1250	1240	1220	1190	1180	1110	7.2	

F, forage type (A v. RW and B); G, grass type; L × F, forage level × forage type interaction (A v. RW and B); L × G, forage level × grass type interaction.

\* For details of diets and procedures, see Tables 1 and 2 and pp. 142–143.

† Seven lambs/treatment, 42 d, based on unshrunk live weight; error df 36.

‡ Five lambs/treatment; error df 26.

type interaction, and forage level × grass type interaction. A regression of digestible organic matter intake (DOMI) v. liver non-fat organic matter (NFOM) mass was conducted. Statistical Analysis System (1985) was used for all analyses.

## RESULTS

Forage composition (Table 2) was generally as expected, with forage A being higher in N than the grasses and a ranking in NDF concentration of  $A < RW < B$ . ADL relative to NDF was 160, 60 and 80 g/kg for forages A, RW and B respectively.

Average DM intake over the entire experiment was similar among low-forage diets, but

Table 4. *Gastrointestinal tract digesta mass (g fresh) for lambs fed on diets of 250 or 750 g lucerne (Medicago sativa; A), ryegrass (Lolium multiflorum)-wheat (Triticum aestivum; RW) or bermudagrass (Cynodon dactylon; B) hay\*†*

(Mean values for five lambs/treatment)

Forage level (L; g/kg)...	250			750			SE	Statistical analysis: effects were significant ( $P < 0.05$ ) for:
	A	RW	B	A	RW	B		
Dietary forage...								
Total	4800	4565	5552	5837	5992	6914	456.3	L,G
Reticulo-rumen	3410	3436	4181	4084	4179	5085	352.1	L,G
Omasum	95	79	104	125	100	170	18.3	L,G
Abomasum	182	138	155	195	233	198	45.1	
Small intestine	520	370	479	609	681	646	59.9	L
Caecum	397	390	453	556	551	611	48.6	L
Large intestine	200	156	184	272	253	208	20.5	L,S

G, grass type; S, sex.

\* For details of diets and procedures, see Tables 1 and 2 and pp. 142–143.

† Error df for large intestine 23; error df for other variables 24.

Table 5. *Mass (g fresh) of tissues of lambs fed on diets of 250 or 750 g lucerne (Medicago sativa; A), ryegrass (Lolium multiflorum)-wheat (Triticum aestivum; RW) or bermudagrass (Cynodon dactylon; B) hay\**

(Mean values for five lambs/treatment)

Forage level (L; g/kg)...	250			750			SE	Statistical analysis: effects were significant ( $P < 0.05$ ) for:
	A	RW	B	A	RW	B		
Dietary forage...								
Gastrointestinal tract								
Total†	1964	2198	2186	2322	2176	2027	116.4	L × F
Reticulo-rumen†	645	687	697	735	667	666	41.4	
Omasum†	78	84	80	92	94	95	8.0	
Abomasum†	173	168	167	182	165	154	14.9	
Small intestine‡	690	777	752	815	805	694	49.4	S
Caecum†	124	157	153	159	140	133	10.8	L × F
Large intestine†	237	308	321	321	288	268	22.6	L × F
Other organs†								
Liver	823	769	783	692	632	503	42.1	L,F
Heart	189	203	181	174	178	170	10.8	
Lungs	455	423	441	464	427	393	37.6	
Kidneys	118	112	114	115	112	100	6.1	
Spleen	77	73	78	73	64	57	5.4	L
Visceral fat‡	1957	1574	1377	958	1219	781	209.4	L,S
All tissues except visceral fat‡	3595	3745	3749	3808	3557	3218	172.7	S

F, forage type (A v. RW and B); L × F, forage level × forage type interaction; S, sex.

\* For details of diets and procedures, see Tables 1 and 2 and pp. 142–143.

† Error df 24.

‡ Error df 23.

with 750 g forage/kg intake tended to be lowest for diet B (forage level × grass type interaction,  $P < 0.10$ ; Table 3). Organic matter digestibility was higher ( $P < 0.05$ ) for low-forage diets than high-forage diets and for diet RW than diet B, especially with 750 g forage/kg (forage level × grass type interaction;  $P < 0.05$ ). DOMI on the 7 d preceding

Table 6. Mass (g non-fat organic matter) of tissues of lambs fed on diets of 250 or 750 g lucerne (*Medicago sativa*; A), ryegrass (*Lolium multiflorum*)–wheat (*Triticum aestivum*; RW) or bermudagrass (*Cynodon dactylon*; B) hay\*†

(Mean values for five lambs/treatment)

Forage level (L; g/kg)...	250			750			SE	Statistical analysis: effects were significant ( $P < 0.05$ ) for:
	A	RW	B	A	RW	B		
Gastrointestinal tract								
Total	259.0	294.9	291.5	303.1	276.6	264.3	13.04	L × F
Reticulo-rumen	92.6	101.9	103.4	106.0	95.0	97.1	5.39	L × F
Omasum	10.9	11.6	10.6	11.8	11.3	11.6	1.12	
Abomasum	20.4	20.9	20.3	21.7	19.1	18.1	1.68	
Small intestine	95.0	109.0	106.6	110.4	106.2	94.9	6.23	L × F
Caecum	16.8	21.2	19.9	21.5	18.2	17.2	1.51	L × F
Large intestine	23.5	30.3	30.8	31.7	27.0	25.4	2.21	L × F
Other organs								
Liver	203.7	196.4	201.6	176.8	156.3	126.5	10.37	F
Heart	27.2	28.8	26.9	26.2	25.5	23.5	1.36	L
Lungs	75.9	72.5	77.4	77.9	71.2	66.0	5.93	
Kidneys	18.9	19.5	17.5	18.6	18.8	15.9	0.86	G
Spleen	14.1	13.3	13.7	13.1	11.4	10.7	0.98	L
All tissues	598.8	625.4	628.7	614.7	559.8	506.9	24.80	L, L × F

F, forage type (A v. RW and B); G, grass type; L × F, forage level × forage type interaction.

\* For details of diets and procedures, see Tables 1 and 2 and pp. 142–143.

† Error df 24.

slaughter was 0.89, 0.83, 0.90, 0.83, 0.77 and 0.61 (SE 0.054) kg/d for diets A-25, RW-25, B-25, A-75, RW-75, and B-75 respectively (forage level and forage level × grass type interaction,  $P < 0.05$ ; forage type,  $P < 0.10$ ). NDF digestibility was lower ( $P < 0.05$ ) for low-forage diets than high-forage diets, for diet A than grass diets, and for diet B than diet RW. N digestibility was higher ( $P < 0.05$ ) for low-forage diets than high-forage diets and for diet B than diet RW. Live-weight gain and gain:feed were higher ( $P < 0.05$ ) for diets with 250 than 750 g forage/kg. Full- and empty-body weights and carcass weight were greater ( $P < 0.05$ ) for 250 than 750 g forage/kg. Backfat depth with 250 g forage/kg ranked A > B > RW, but with 750 g forage/kg the ranking was RW > A and B (forage level × forage type and forage level × grass type interactions;  $P < 0.05$ ). *Longissimus dorsi* area was similar among diets.

Fresh digesta mass in the total GIT was approximately 1 kg higher ( $P < 0.05$ ) for diet B than diet RW with both forage levels primarily because of the higher ( $P < 0.05$ ) quantity of digesta in the reticulo-rumen (Table 4). Digesta mass in all GIT components except the abomasum was greater ( $P < 0.05$ ) for 750 than 250 g forage/kg diets.

Fresh tissue mass is given in Table 5; tissue non-fat organic matter (NFOM; g, g/kg EBW and g/kg DOMI) is shown in Tables 6, 7 and 8 respectively. NFOM (g) of GIT segments except the omasum and abomasum was lower for diet A than for grass diets with 250 g forage/kg but higher for diet A with forage at 750 g/kg diet (forage level × forage type interaction;  $P < 0.05$ ). Total GIT, reticulo-rumen and omasum NFOM were lower ( $P < 0.05$ ) for diet A than for grass diets and similar for diets A and RW with 250 g forage/kg but higher for diet B than for diet RW with forage at 750 g/kg diet (forage level × grass type interaction;  $P < 0.05$ ).

Liver NFOM (g) was higher ( $P < 0.05$ ) for 250 than 750 g forage/kg diets; liver NFOM (g) was similar among forage sources with 250 g forage/kg but tended to rank A > RW >

Table 7. *Mass (g non-fat organic matter/kg empty-body weight) of tissues of lambs fed on diets of 250 or 750 g lucerne (Medicago sativa; A), ryegrass (Lolium multiflorum)-wheat (Triticum aestivum; RW) or bermudagrass (Cynodon dactylon; B) hay\**†

(Mean values for five lambs/treatment)

Forage level (L; g/kg) ...	250			750			SE	Statistical analysis: effects were significant ( $P < 0.05$ ) for:
	A	RW	B	A	RW	B		
Dietary forage ...								
Gastrointestinal tract								
Total	6.73	8.07	7.84	9.16	8.07	8.88	0.420	L, L × F
Reticulo-rumen	2.40	2.78	2.78	3.20	2.72	3.28	0.174	L, L × F
Omasum	0.28	0.31	0.28	0.36	0.33	0.39	0.034	L
Abomasum	0.53	0.57	0.55	0.66	0.56	0.60	0.044	
Small intestine	2.47	2.99	2.87	3.33	3.10	3.17	0.195	L
Caecum	0.43	0.58	0.54	0.65	0.53	0.58	0.048	L × F
Large intestine	0.61	0.83	0.83	0.96	0.79	0.86	0.070	L × F
Other organs								
Liver	5.30	5.35	5.40	5.32	4.55	4.22	0.231	L, F, L × F
Heart	0.71	0.79	0.72	0.80	0.74	0.78	0.043	
Lungs	1.98	1.99	2.08	2.30	2.08	2.21	0.159	
Kidneys	0.49	0.53	0.47	0.56	0.55	0.53	0.026	L
Spleen	0.37	0.36	0.37	0.40	0.33	0.36	0.026	
All tissues	15.57	17.10	16.87	18.52	16.33	16.98	0.655	L × F

F, forage type (A v. RW and B); L × F, forage level × forage type interaction.

\* For details of diets and procedures, see Tables 1 and 2 and pp. 142–143.

† Error df 24.

Table 8. *Mass (g non-fat organic matter/kg digestible organic matter intake) of tissues of lambs fed on diets of 250 or 750 g lucerne (Medicago sativa; A), ryegrass (Lolium multiflorum)-wheat (Triticum aestivum; RW) or bermudagrass (Cynodon dactylon; B) hay\**

(Mean values for five lambs/treatment)

Forage level (L; g/kg) ...	250			750			SE	Statistical analysis: effects were significant ( $P < 0.05$ ) for:
	A	RW	B	A	RW	B		
Dietary forage ...								
Gastrointestinal tract†								
Total	2.91	3.60	3.32	3.75	3.59	4.43	0.227	L, F, L × G
Reticulo-rumen	1.04	1.23	1.18	1.30	1.24	1.63	0.076	L, F, G, L × G
Omasum	0.12	0.14	0.12	0.14	0.15	0.19	0.013	L, L × G
Abomasum	0.23	0.25	0.23	0.27	0.25	0.30	0.020	L
Small intestine	1.07	1.34	1.22	1.36	1.38	1.60	0.111	L
Caecum	0.19	0.26	0.23	0.27	0.23	0.29	0.024	
Large intestine	0.26	0.38	0.35	0.40	0.35	0.43	0.037	
Other organs								
Liver‡	2.29	2.39	2.27	2.17	2.02	2.11	0.105	L
Heart‡	0.31	0.35	0.30	0.33	0.33	0.40	0.030	
Lungs‡	0.86	0.88	0.87	0.93	0.93	1.13	0.083	
Kidneys‡	0.21	0.24	0.20	0.23	0.24	0.27	0.013	L, L × G
Spleen‡	0.16	0.16	0.16	0.16	0.15	0.18	0.015	
All tissues‡	6.74	7.62	7.12	7.57	7.26	8.52	0.392	L × G

F, forage type (A v. RW and B); G, grass type; L × G, forage level × grass type interaction.

\* For details of diets and procedures, see Tables 1 and 2 and pp. 142–143.

† Error df 24.

‡ Error df 23.

B with 750 g forage/kg (forage level  $\times$  forage-type and forage level  $\times$  grass type interactions;  $P < 0.10$ ). Liver NFOM (g/kg EBW) was similar between forage levels with diet A but lower for 750 than 250 g forage/kg with diets RW and B (forage level  $\times$  forage type interaction;  $P < 0.05$ ). Liver NFOM (g/kg DOMI) was higher ( $P < 0.05$ ) for 250 than 750 g forage/kg.

Heart NFOM was higher ( $P < 0.05$ ) for 250 than 750 g forage/kg when expressed in g but not when expressed in g/kg EBW; lung mass was not affected by dietary treatment. Kidney NFOM (g) was higher ( $P < 0.05$ ) for diet RW than for diet B; whereas, when expressed in g NFOM/kg EBW kidney mass was higher ( $P < 0.05$ ) with 750 than 250 g forage/kg. Spleen mass (g fresh and NFOM) was higher ( $P < 0.05$ ) for 250 than 750 g forage/kg.

## DISCUSSION

### *Intake*

Lower DM intake for diet B than for diet RW at 750 g/kg diet agrees with higher ingestion of temperate than tropical grasses in other studies (Lagasse *et al.* 1990; Galloway *et al.* 1991; Sun *et al.* 1991). Primarily because of the lower cell wall concentration and more rapid rumen digestion of cell walls and rate of passage of particulate matter, legume intake often is greater than that of temperate grass (Reid *et al.* 1990; Goering *et al.* 1991; Thomson *et al.* 1991; Cruickshank *et al.* 1992). Voluntary intake averaged over the entire experiment was similar for diets A and RW with 750 g forage/kg, but intake during the last week of the experiment was slightly greater for diet A (1.19 *v.* 1.09 kg/d). Similar DM intake among low-forage diets signifies little impact of forage source on intake when comprising 250 g/kg diet.

### *Digesta mass*

In agreement with Jahn *et al.* (1976), GIT digesta mass was greater for the high than for the low dietary forage level. Digesta mass influences differences in live-weight gain between ruminants fed on forage- and concentrate-based diets (Jahn *et al.* 1970; Jahn & Chandler, 1976; Bailey, 1986). Forage type did not affect GIT digesta mass except for a higher quantity of digesta in the large intestine for diet A *v.* grass diets. In contrast, Waldo *et al.* (1990) observed higher digesta mass in steers consuming orchardgrass than lucerne silage at approximately 65 or 90 g DM/kg body weight<sup>0.75</sup>. These levels of intake are comparable to two treatment means in our experiment (63 to 76 g DM/kg body weight<sup>0.75</sup>); however, the NDF level of their lucerne silage was considerably lower than that in diet A used here. Also, faster rumen passage rate of particulate matter for legumes than for grasses could have greater potential to affect digesta mass with restricted than with *ad lib.* consumption.

### *Tissue mass: diet A v. grass diets*

High metabolic activity and positioning between the GIT lumen and periphery allow marked impact of the GIT and liver on nutrient availability to extrasplanchnic tissues (Ferrell, 1988; McBride & Kelly, 1990). Organ mass was measured in the present study as an index of the quantity of energy and nutrients consumed by internal organs and, thus, becoming available to the periphery. Of the measures of organ mass in our study, NFOM, consisting primarily of nitrogenous compounds such as protein, should provide strongest indications of internal organ energy consumption. In this regard, lower total GIT mass for diet A than for grass diets with 250 g forage/kg suggests lower energy use by the GIT; whereas differences in GIT mass between forage types with 750 g forage/kg imply a greater quantity of nutrients being consumed by the GIT with diet A than with grass diets.

Differences between diet A and grass diets in mass of both the reticulo-rumen and intestinal tissues contributed to interactions between forage type and level. Similar total



GIT NFOM:DOMI for diets A-75 and RW-75 suggests that DOMI may have been responsible for the difference in GIT mass (g NFOM) with 750 g forage/kg; whereas dissimilar values with 250 g forage/kg imply the involvement of other factors. These results seem to reflect a threshold relationship, in that elevated GIT mass for grass diets relative to diet A occurred only with the lower quantity of fibre in the GIT with 250 g forage/kg.

Johnson *et al.* (1990) summarized that dietary effects on GIT mass occur through functional workload, relating to the quantity of nutrients absorbed. Webster (1980) suggested that volatile fatty acids, particularly acetate and butyrate, interact with particulate matter in the GIT in effects on mass of, and energy consumed by, the GIT. In support, Rompala *et al.* (1990) increased stomach weight of lambs by adding 100 g polyethylene powder/kg to a 720 g concentrate/kg diet, but insertion of eight polyurethane cubes (22 × 30 × 35 mm) into the rumen did not affect stomach weight regardless of dietary polyethylene inclusion. In a similar experiment, Rompala *et al.* (1988) fed lambs on 720 g concentrate/kg diets with 0 or 100 g polyethylene/kg and increased the weight of the large intestine, stomach complex and lungs, without affecting small intestinal weight. These findings and measures of GIT mass in our experiment suggest that the physical nature of digesta with high-concentrate diets can affect the mass of the GIT, both of the reticulo-rumen and intestinal segments, independent of energy intake and nutrient absorption.

Forage characteristics possibly responsible for differences in GIT mass between diet A and grass diets with 250 g forage/kg are unclear. However, the physical nature and behaviour of legume particles in the rumen differ from grasses. For instance, legume particles are cuboidal in shape compared with the cylindrical nature of grass particles (Troelsen & Campbell, 1968; Moseley & Jones, 1984; Chai *et al.* 1985); rate of change in density is more rapid for legume than grass particles (Hooper & Welch, 1985).

Regression analysis indicated that 76% of variability in liver NFOM (g) was associated with that in DOMI. Thus, part of the difference in liver NFOM between diets A and RW with 750 g forage/kg can be explained by higher DOMI. However, magnitudes of difference between diets A-75 and RW-75 and liver NFOM (g and g/kw EBW) were greater than that in DOMI. The mass of the GIT and the liver are both affected by energy intake, partly because of the general relationship between nutrient absorption and flow to the liver (Johnson *et al.* 1990). However, because GIT metabolic activity is high, liver metabolism encompasses service functions for other tissues, and N transfer between the GIT and liver is extensive (Ferrell, 1988), GIT mass or metabolic activity could directly affect liver mass independent of energy intake. Such a relationship may have contributed to higher liver NFOM (g/kg EBW) for diet A than for diet RW with 750 g forage/kg.

#### *Tissue mass: diet RW v. diet B*

Higher stomach component NFOM:DOMI for diet B than for diet RW with 750 g forage/kg may have been associated with higher digesta mass. Conversely, with 250 g forage/kg GIT digesta mass was higher for diet B than for diets A and RW yet GIT mass was similar among forage sources. These results indicate that with a predominantly tropical grass diet, nutrient and energy consumption by the GIT may account for greater proportions of whole-body energy consumption and DOMI than with a temperate-grass-based diet. Hence, besides typically lower energy intake with tropical- than temperate-grass diets, GIT metabolism may further restrict peripheral nutrient availability.

#### *Tissue mass: 250 v. 750 g forage/kg*

The total GIT NFOM:DOMI was similar for 250 and 750 g forage/kg levels with diet RW but not with diets A or B, possibly in relation to the high NDF digestibility of RW diets. Total GIT NFOM:DOMI was considerably higher for 750 than 250 g forage/kg with diets

A and B primarily because of high GIT mass and low DOMI respectively. Thus, elevated digesta mass for 750 v. 250 g forage/kg may have stimulated intestinal tissue mass with diets A and B, although no influence was evident with diet RW. Reynolds *et al.* (1991) fed growing beef heifers on 250 or 750 g A/kg diets at similar levels of metabolizable energy intake. Portal-drained viscera O<sub>2</sub> consumption at both levels of intake was approximately 23% greater for 750 g forage/kg than for 250 g forage/kg.

#### Summary

Higher GIT mass for diet A than for grass diets at 750 g/kg diet appeared a response to DOMI, whereas lower GIT mass for diet A than for grass diets with 250 g forage/kg may have been caused by differences in characteristics of forage digesta independent of energy intake and digesta mass. With 750 g forage/kg, higher digesta mass for diet B than for diet RW seemed responsible for higher reticulo-rumen mass relative to DOMI. Grass type did not affect GIT mass with 250 g forage/kg even though digesta mass differed. Higher intestinal digesta mass for 750 than for 250 g forage/kg may have elicited higher intestinal tissue mass with diets A and B but not with diet RW, for which NDF digestibility was highest. Liver mass varied primarily with DOMI, although with 750 g forage/kg higher GIT mass for diet A than for grass diets may have had a slight stimulatory effect. Liver mass relative to DOMI was greater for 250 than 750 g forage/kg diets.

#### REFERENCES

- Association of Official Analytical Chemists (1984). *Official Methods of Analysis*, 14th ed. Washington, DC: Association of Official Analytical Chemists.
- Bailey, C. B. (1986). Growth of digestive organs and their contents in Holstein steers: relation to body weight and diet. *Canadian Journal of Animal Science* **66**, 653–661.
- Chai, K., Kennedy, P. M., Milligan, L. P. & Mathison, G. W. (1985). Effects of cold exposure and plant species on forage intake, chewing behavior and digesta particle size in sheep. *Canadian Journal of Animal Science* **65**, 69–76.
- Cherney, D. J. R., Paterson, J. A. & Cherney, J. H. (1989). Use of 2-ethoxy-ethanol and alpha-amylase in the neutral detergent fiber method of feed analysis. *Journal of Dairy Science* **72**, 3079–3084.
- Cruickshank, G. J., Poppi, D. P. & Sykes, A. R. (1992). The intake, digestion and protein degradation of grazed herbage by early-weaned lambs. *British Journal of Nutrition* **68**, 349–364.
- Ferrell, C. L. (1988). Energy metabolism. In *The Ruminant Animal. Digestive Physiology and Nutrition*, pp. 250–268 [D. C. Church, editor]. Englewood Cliffs, NJ: Prentice Hall.
- Ferrell, C. L., Koong, L. J. & Nienaber, J. A. (1986). Effect of previous nutrition on body composition and maintenance energy costs of growing lambs. *British Journal of Nutrition* **56**, 595–605.
- Galloway, D. L. Sr, Goetsch, A. L., Forster, L. A. Jr, Sun, W. & Johnson, Z. B. (1991). Feed intake and digestion by Holstein steers fed warm or cool season grass hays with corn, dried molasses or wheat middlings. *Journal of Dairy Science* **74**, 1038–1046.
- Goering, H. K. & Van Soest, P. J. (1970). *Forage Fiber Analyses. Apparatus, Reagents, Procedures and Some Applications. Agricultural Handbook* no. 379, pp. 1–12. Washington, DC: US Department of Agriculture.
- Goering, H. K., Waldo, D. R., Tyrrell, H. F. & Thomson, D. J. (1991). Composition of formaldehyde- and formic acid-treated alfalfa and orchardgrass silages harvested at two maturities and their effects on intake and growth by Holstein heifers. *Journal of Animal Science* **69**, 4634–4643.
- Hooper, A. P. & Welch, J. G. (1985). Effects of particle size and forage composition on functional specific gravity. *Journal of Dairy Science* **68**, 1181–1188.
- Jahn, E. & Chandler, P. T. (1976). Performance and nutrient requirements of calves fed varying percentages of protein and fiber. *Journal of Animal Science* **42**, 727–735.
- Jahn, E., Chandler, P. T. & Kelly, R. F. (1976). Nutrient accumulation and prediction of body composition of 20-week-old calves fed varying percentages of protein and fiber. *Journal of Animal Science* **42**, 736–744.
- Jahn, E., Chandler, P. T. & Polan, C. E. (1970). Effects of fiber and ratio of starch to sugar on performance of ruminating calves. *Journal of Dairy Science* **53**, 466–474.
- Johnson, D. E., Johnson, K. A. & Baldwin, R. L. (1990). Changes in liver and gastrointestinal tract energy demands in response to physiological workload in ruminants. *Journal of Nutrition* **120**, 649–655.
- Johnson, L. R. (1988). Regulation of gastrointestinal mucosal growth. *Physiological Reviews* **68**, 456–502.
- Jung, H. G. & Fahey, G. C. Jr (1983). Nutritional implications of phenolic monomers and lignin: a review. *Journal of Animal Science* **57**, 206–219.

- Lagasse, M. P., Goetsch, A. L., Landis, K. M. & Foster, L. A. Jr (1990). Effects of supplemental alfalfa hay on feed intake and digestion by Holstein steers consuming high-quality bermudagrass or orchardgrass hay. *Journal of Animal Science* **68**, 2839–2847.
- McBride, B. W. & Kelly, J. M. (1990). Energy cost of absorption and metabolism in the ruminal gastrointestinal tract and liver: a review. *Journal of Animal Science* **68**, 2997–3010.
- McBride, B. W. & Milligan, L. P. (1984). The effect of lactation on ouabain-sensitive respiration of the duodenal mucosa of cows. *Canadian Journal of Animal Science* **64**, 317–324.
- Mertens, D. R. & Lofton, J. R. (1980). The effect of starch on forage fiber digestion kinetics in vitro. *Journal of Dairy Science* **63**, 1437–1446.
- Minson, D. J. (1990). *Forage in Ruminant Nutrition*. San Diego, CA: Academic Press.
- Moseley, G. & Jones, J. R. (1984). The physical digestion of perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) in the foregut of sheep. *British Journal of Nutrition* **52**, 381–390.
- Reid, R. L., Jung, G. A., Cox-Ganser, J. M., Rybeck, B. F. & Townsend, E. C. (1990). Comparative utilization of warm- and cool-season forages by cattle, sheep and goats. *Journal of Animal Science* **68**, 2986–2994.
- Reynolds, C. K., Tyrrell, H. F. & Reynolds, P. J. (1991). Effects of diet forage-to-concentrate ratio and intake on energy metabolism in growing beef heifers: net nutrient metabolism by visceral tissues. *Journal of Nutrition* **121**, 1004–1012.
- Rompala, R. E., Hoagland, T. A. & Meister, J. A. (1988). Effect of dietary bulk on organ mass, fasting heat production and metabolism of small and large intestines in sheep. *Journal of Nutrition* **188**, 1153–1157.
- Rompala, R. E., Hoagland, T. A. & Meister, J. A. (1990). Modifications in growth and morphology of ovine jejunal and ruminal epithelia as affected by inert dietary substances. *Journal of Animal Science* **68**, 2530–2535.
- Statistical Analysis System (1985). *SAS User's Guide: Statistics*. Cary, NC: SAS Institute Inc.
- Sun, W., Goetsch, A. L., Forster, L. A. Jr, Galloway, D. L. Sr & Johnson, Z. B. (1991). Feed intake and digestion by Holstein steer calves consuming bermudagrass or ryegrass-wheat hay and supplemented with alfalfa, corn or monensin. *Animal Feed Science and Technology* **34**, 241–254.
- Thomson, D. J., Waldo, D. R., Goering, H. K. & Tyrrell, H. F. (1991). Voluntary intake, growth rate, and tissue retention by Holstein steers fed formaldehyde- and formic acid-treated alfalfa and orchardgrass silages. *Journal of Animal Science* **69**, 4644–4659.
- Troelsen, J. E. & Campbell, J. B. (1968). Voluntary consumption of forages by sheep and its relation to the size and shape of particles in the digestive tract. *Animal Production* **10**, 289–296.
- Waldo, D. R., Varga, G. A., Huntington, G. B., Glenn, B. P. & Tyrrell, H. F. (1990). Energy components of growth in Holstein steers fed formaldehyde- and formic acid-treated alfalfa or orchardgrass silages at two intakes. *Journal of Animal Science* **68**, 3792–3804.
- Webster, A. J. F. (1980). Energy cost of digestion and metabolism in the gut. In *Digestive Physiology and Metabolism in Ruminants*, pp. 469–484 [Y. Ruckebusch and P. Thivend, editors]. Westport, CT: AVI Publ. Co., Inc.
- Williams, C. H., David, D. J. & Iismaa, O. (1962). The determination of chromic oxide in feces samples by atomic absorption spectrophotometry. *Journal of Agricultural Science, Cambridge* **59**, 381–385.
- Windham, W. R., Amos, H. E. & Evans, J. J. (1987). Hemicellulose digestibility by steers fed sun-cured hay and drum-dehydrated alfalfa and coastal bermuda grass. *Journal of Agricultural and Food Chemistry* **35**, 698–704.