Net flux of nutrients across splanchnic tissues in wethers consuming grasses of different sources and physical forms *ad libitum**†

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Crossbred sheep (*n* 16, 8·5 months of age and 33 (SE 0·9) kg) were used in a 21 d experiment (2×2 factorial) to determine effects on net flux of nutrients across the portal-drained viscera (PDV) and liver of *ad libitum* consumption of bermudagrass (*Cynodon dactylon*; B) *v.* ryegrass (*Lolium multiflorum*)–wheat (*Triticum aestivum*; RW) hay, coarsely chopped (CC) or finely ground and pelleted (GP). Crude protein concentrations were 86, 81, 113 and 119 g/kg and neutral-detergent fibre concentrations were 710, 688, 654 and 672 g/kg (dry matter basis) for B-CC, B-GP, RW-CC and RW-GP respectively. Digestible energy intake (6·0, 9·6, 10·2 and 13·8 MJ/d) differed ($P < 0·01$) with grass source and form, and digestible N intake values were 4·4, 7·0, 8·4 and 14·1 (SEM 0·82) g/d for B-CC, B-GP, RW-CC and RW-GP diets respectively. Consumption of O_2 by the PDV (118, 165, 144 and 155 mmol/h) and splanchnic bed (196, 273, 247 and 266 mmol/h for B-CC, B-GP, RW-CC and RW-GP respectively) was greater ($P = 0·07$) for GP than for CC. The ratio splanchnic heat energy production : digestible energy intake was greater ($P = 0·06$) for B than for RW (0·374, 0·300, 0·278 and 0·219 for B-CC, B-GP, RW-CC and RW-GP respectively). α-Amino-N release by the PDV ($P < 0·01$; 11·6, 12·8, 23·0 and 18·7 mmol/h) and uptake by the liver ($P = 0·07$; 15·2, 6·1, 17·0 and 19·3 mmol/h for B-CC, B-GP, RW-CC and RW-GP respectively) were greater for RW than for B. Release of NH_3-N by the PDV was greater ($P = 0·02$) for CC than for GP (12·5, 6·2, 15·7 and 8·9 mmol/h), and hepatic urea-N release differed between grass sources ($P = 0·03$) and physical forms ($P = 0·07$; 22·6, 12·7, 31·4 and 24·8 mmol/h for B-CC, B-GP, RW-CC and RW-GP respectively). In conclusion, decreases in forage particle size elicited by grinding and pelleting did not affect the difference between grass sources in splanchnic tissue heat energy production relative to digestible energy intake.

Forage: Splanchnic metabolism: Sheep

Effects of fine grinding and pelleting forage on ruminant performance are often not explained solely by changes in absorbed nutrients (Berger *et al.* 1994), implying an improved efficiency of metabolism. The grinding and pelleting of forage decreases eating time per unit of intake, and whole-body energy expenditure is markedly increased during eating (Webster, 1980). Grinding and pelleting also has, in some instances, increased ruminal propionate concentration (Fahey *et al.* 1993; Berger *et al.* 1994), which conceivably, with

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constant hepatic glucose release, could lessen hepatic energy use and uptake of amino acids for gluconeogenesis (Seal & Reynolds, 1993). Grinding and pelleting has not consistently altered microbial protein synthesized per unit of organic matter fermented; therefore, a marked change in the ratio absorbed energy:amino acids is not expected. Whether effects of grinding and pelleting forage on gut metabolism of amino acids parallel those on energy use is unclear. However, an increased potential for amino acid use by peripheral tissues and, hence, possibly decreased hepatic uptake of amino acids, might be facilitated by grinding and pelleting if increased peripheral energy availability allows enhanced protein synthesis.

Lower digestibility of tropical than temperate grass results in lower absorption of both energy and amino acids, although in many instances peripheral availability of energy appears to be relatively more limiting to tissue accretion than that of amino acids (Galyean & Goetsch, 1993). Because eating time relates directly to dietary cell-wall concentration (Dulphy *et al.* 1980), it is anticipated that tropical grass diets elicit greater energy use for ingestion than temperate grasses. Unique proportions and arrangements of specific plant tissues in tropical and temperate grasses may contribute to greater gut digesta mass for tropical grass and differences in the nature of digesta (Wilson, 1993). Sun *et al.* (1994) and Kouakou *et al.* (1995*b*) largely attributed differences in gut tissue mass among diets varying in concentrate level or forage quality to gut digesta mass, and direct effects of gut tissue mass on that of the liver, independent of the influence of digestible organic matter intake, were suggested also (Kouakou *et al.* 1995*a*,*b*). Differences between forage sources in gut tissue mass and energy use will result in peripheral tissue energy availability deviating from expectations based solely on intake and digestibility. The extent to which differences between tropical and temperate grasses in splanchnic tissue metabolism and ingestive energy use affect energy *v.* amino acid availability to peripheral tissues is unknown.

It is unclear if physical characteristics of tropical and temperate grasses altered by fine grinding and pelleting elicit differences in splanchnic tissue metabolism. The absence or presence and nature of such interactions may aid in understanding forage characteristics responsible for differences in splanchnic metabolism and, thus, in whole-body metabolism. Therefore, the objectives of our experiment were to determine differences in net flux of O_2 and nutrients across the portal-drained viscera (PDV) and liver with *ad libitum* consumption of tropical *v.* temperate grass, coarsely chopped or finely ground and pelleted.

MATERIALS AND METHODS

Sixteen crossbred (Suffolk × Ramboillet-Dorset) wethers (33 (SE 0·9) kg body weight; 8·5 months of age) were surgically fitted with chronic indwelling catheters in a hepatic vein, the portal vein and a mesenteric vein and artery (Ferrell *et al.* 1992). Catheters were filled with heparinized (100 U/ml) saline (0·85 mol/l) solution at surgery. The sheep began the experiment approximately 5 weeks after surgery, being previously used in a 23 d experiment (Goetsch *et al.* 1996) with *ad libitum* consumption of different mixtures of the same sources of grass hay used in the present experiment. To avert or minimize effects of treatments in the previous experiment on results in the present one, wethers were allocated to treatments for equal distribution relative to previous treatments. This involved subjecting one wether from each of the four previous treatments to each treatment in the present experiment. Sheep were individually maintained in 1·1 × 1·5 m elevated pens with

an expanded metal floor and free access to water. Sheep were cared for in accordance with the guidelines of Consortium (1988).

Diets were prepared from a bermudagrass hay (B; *Cynodon dactylon*; harvested at the vegetative stage of growth) or a ryegrass–wheat hay (RW; composed of *Lolium multiflorum* (harvested at the late-vegetative to boot stage of growth) and *Triticum aestivum* (harvested at the post-anthesis to early milk stage)). Diets were offered either coarsely chopped (B-CC; RW-CC) or finely ground and pelleted (B-GP; RW-GP) at 1·05–1·10 g/g of consumption on the preceding 2–4 d. Grinding was through a 1·6 mm screen and pellets were formed with a 4·8 mm die. Temperature during pelleting was slightly greater for B than for RW (60 *v.* 45°), with hay subjected to steam for approximately 45 s. Equal-sized meals were given to sheep at 14.00, 22.00 and 06.00 hours and at 14.00 hours sheep received 3·5 g of a mineral mixture containing 200 g trace minerals/kg and 800 g salt/kg. The trace mineral mixture contained (mg/g): Zn 120, Mn 100, K 50, Mg 25, Cu 15, I 3, Co 1 and Se 0·2.

The experiment was 21 d in length. Feed was sampled daily on days 11–21 and combined to form a composite. In addition, ground hay was sampled before pelleting for mean particle size determination. Percentages of time in a 24 h period spent standing *v.* lying, eating, ruminating or idle (time not spent eating or ruminating) were determined by observation at 15 min intervals on day 13. Grab samples of faeces were collected on days 14–17, at 12 h intervals advancing 3 h daily. Samples were frozen between collections, dried at 55°, ground to pass a 2 mm screen and used to form a composite. Rumen fluid was obtained by stomach tube on day 16 at 09.00 hours, strained through cheesecloth, acidified with 3·6 M-H_2SO_4 (1 ml/100 ml rumen fluid), frozen and later analysed for NH_3-N (Broderick & Kang, 1980).

Metabolism cages were used to house sheep during blood collections, with four sheep sampled daily (one per treatment; chosen randomly within treatment) on days 18–21. Sheep were accustomed to metabolism cages because of prior exposure to these conditions and displayed normal intake and other activities while in cages. A priming dose (15 ml) of *p*-aminohippuric acid (22·5 g/l) was given at 07.30 hours into the mesenteric vein catheter, followed by continuous infusion (0·8 ml/min) until 15.25 hours. The priming dose and infusion were through a 0·2 μm sterile filter. Body weight was determined immediately after the last sample was obtained.

Blood was withdrawn at 08.00, 09.00, 10.00, 11.00, 12.00, 12.00, 14.00 and 15.00 hours with a 10 min interval between sheep and representing an entire 8 h feeding interval. The treatment order for sampling differed among days. A blood sample (1 ml) was obtained anaerobically into a heparinized syringe and placed in ice for immediate measurement of packed cell volume and O_2 concentration (OSM 2; Radiometer Corporation, Copenhagen, Denmark) as described by Eisemann & Nienaber (1990). Additionally, a 10 ml sample was taken in a tube with potassium oxalate and NaF and placed in ice, from which a 1·5 ml portion was diluted with deionized water (4·5 ml) for the same-day analysis of *p*-aminohippuric acid, α-amino-N (AAN), urea-N (UN) and NH_3-N, as described by Eisemann & Nienaber (1990). Concentrations of *p*-aminohippuric acid, AAN, UN, NH_3-N and packed cell volume were averaged across time for calculation of blood flows and metabolite fluxes. Packed cell volume was used to estimate plasma flows. Remaining blood of the 10 ml sample was used to form a composite across sampling times. Plasma for glucose analysis (Sigma Diagnostics, procedure no. 315; Sigma Chemical Co., St. Louis, MO, USA) was harvested via centrifugation. Deproteinized blood ($Ba(OH)_2$ and $ZnSO_4$) was used for analysis of propionate (Yen *et al.* 1991), except that iso-caproic acid was added as an internal standard before GC. Deproteinized blood ($HClO_4$; Harmon *et al.* 1991)

was used to determine the concentration of L-lactate (Gutmann & Wahlefeld, 1974). Net metabolite fluxes were calculated based on venoarterial concentration differences and whole blood or plasma flows (Burrin *et al.* 1991).

Faecal composites were dried at 55° and allowed to air-equilibrate. Hay and faecal samples were ground to pass a 1 mm screen and analysed for DM, ash, Kjeldahl N, energy (Association of Official Analytical Chemists, 1984), neutral-detergent fibre (Goering & Van Soest, 1970; without sodium sulphite, decalin or ethoxyethanol) and acid-insoluble ash (2 M-HCl; Van Keulen & Young, 1977). Hay samples were also analysed for acid-detergent fibre (non-sequential), acid-detergent lignin, acid-detergent fibre-N (Goering & Van Soest, 1970) and N soluble in 0·15 M-NaCl (Waldo & Goering, 1979). Cellulose was estimated as loss in weight on H_2SO_4 treatment and hemicellulose as the difference between neutral-detergent- and acid-detergent fibre. The average of feed intake on day 12 through to the day of blood sampling was used to calculate digestibilities, with use of acid-insoluble ash as an internal, inert marker. Hay sampled after grinding but before pelleting was sieved through screen apertures of 4·75, 2·36, 1·18, 0·60, 0·30, 0·15, 0·075 and 0 mm to determine mean particle size.

Data were analysed as a completely random design by ANOVA and the general linear models procedure of Statistical Analysis Systems (1990). Treatment allotment and sampling day assignment of wethers were conducted to avoid treatment bias; thus, these factors were not considered statistically. Orthogonal contrasts were used to test effects of grass source (B *v.* RW), form (CC *v.* GP) and their interaction. The general linear models procedure was used for most regressions, and the regression procedure of Statistical Analysis Systems (1990) was used to determine partial regression coefficients. Hepatic and splanchnic fluxes were not calculated for one wether because of a non-patent hepatic catheter. Therefore, the number of observations was sixteen for feed intake, digestibility, rumen fluid concentration of NH_3-N, behaviour, metabolite concentrations in arterial and portal blood and PDV net fluxes; fifteen observations were derived for hepatic venous blood concentrations of metabolites and hepatic and splanchnic net fluxes. Differences were considered significant with $P \leq 0{\cdot}10$.

RESULTS AND DISCUSSION

Forage composition

Composite samples of feedstuffs were subjected to laboratory analyses; therefore, these data were not statistically analysed. Concentrations of crude protein and fibre fractions were not markedly altered by grinding and pelleting (Table 1). Heat generated in grinding and/or pelleting increased acid-detergent-fibre N concentration more with RW than B, although the decline in soluble N concentration was of similar magnitude for both grass sources. Consequently, a small increase with grinding and pelleting in insoluble available N occurred for B, but a decrease was noted for RW. Mean particle sizes were 0·45 and 0·54 mm for B-GP and RW-GP respectively.

Intake, digestibility, rumen ammonia-nitrogen concentration and behaviour

DM intake was greater ($P < 0{\cdot}01$) for RW than for B and for ground and pelleted than for coarsely chopped grass, with a slightly greater difference between physical forms than grass sources (Table 2). The effect of grinding and pelleting on DM intake (0·57 fractional increase) was greater than noted by Greenhalgh & Reid (1973; 0·45 fractional increase). Effects of grinding and pelleting on intake have been shown to vary among forages (Berger

Table 1. *Grass hay composition (dry matter basis)*

Constituent	Bermudagrass		Ryegrass–wheat	
	Coarsely chopped	Ground and pelleted	Coarsely chopped	Ground and pelleted
Ash (g/kg)	68	65	80	82
Crude protein (g/kg)	86	81	113	119
Energy (MJ/kg)	16·6	16·7	16·9	17·6
Neutral-detergent fibre (g/kg)	710	688	654	672
Acid-detergent fibre (g/kg)	326	303	356	342
Acid-detergent lignin (g/kg)	61	54	47	44
Cellulose (g/kg)	263	247	307	294
Hemicellulose (g/kg)	384	385	298	330
Acid-detergent fibre-N (g/kg total N)	115	158	57	150
Soluble N (g/kg total N)	653	580	571	535
Insoluble available N (g/kg total N)	232	262	382	315

Table 2. *Feed intake and digestion by wethers consuming bermudagrass or ryegrass–wheat hay coarsely chopped or ground and pelleted**

(Mean values and pooled standard error for four sheep per dietary group)

Variable	Bermudagrass		Ryegrass–wheat		SEM†	Statistical significance of effect of:‡
	Coarsely chopped	Ground and pelleted	Coarsely chopped	Ground and pelleted		
Dry matter intake (g/d)	665	1123	923	1370	79·0	G, F
Organic matter						
Intake (g/d)	620	1050	849	1257	73·1	G, F
Digestion						
g/kg	561	530	668	584	33·9	G
g/d	343	556	573	736	51·3	G, F
Energy						
Intake (MJ/d)	11·1	18·7	15·6	24·1	1·35	G, F
Digestion						
kJ/MJ	551	516	650	571	3·34	G
MJ	6·0	9·6	10·2	13·8	0·91	G, F
Nitrogen						
Intake (g/d)	9·1	14·5	16·7	26·1	1·33	G, F
Digestion						
g/kg	495	486	496	540	3·99	
g/d	4·4	7·0	8·4	14·1	0·82	G, F, i
Neutral-detergent fibre						
Intake (g/d)	477	773	604	921	53·5	G, F
Digestion						
g/kg	533	471	694	577	3·53	G, F
g/d	247	364	423	533	37·2	G, F

* For details of diets and procedures, see Table 1 and pp. 770–772.

† Error df 12.

‡ G, grass source (bermudagrass *v.* ryegrass–wheat; $P < 0·05$); F, grass form (coarsely chopped *v.* ground and pelleted; $P < 0·05$); i, interaction between grass source and form ($P < 0·10$).

et al. 1994). For example, Coleman *et al.* (1978) observed slightly greater effects of grinding and pelleting on intake of paragrass (*Brachiaria mutica*) than of St Augustinegrass (*Stenotaphrum secundatum*) and on intake of grasses harvested after 8 weeks of regrowth than after 4 weeks. However, in the present experiment grinding and pelleting had a comparable effect on intake of both grass sources.

Organic matter digestibility was greater ($P = 0{\cdot}03$) for RW than for B and tended ($P = 0{\cdot}11$) to be decreased by grinding and pelleting (Table 2). Consequently, digestible energy intake (DEI) was considerably greater for RW than for B ($P < 0{\cdot}01$) and for ground and pelleted than for coarsely chopped grass ($P < 0{\cdot}01$). Total tract N digestibility was similar among treatments. An interaction ($P = 0{\cdot}08$) between grass source and form occurred, with digestible N intake being increased by grinding and pelleting to a slightly greater extent with RW than B.

Neutral-detergent fibre digestibility was lower for B than for RW ($P < 0{\cdot}01$) and for ground and pelleted than for coarsely chopped grass ($P = 0{\cdot}03$), although no statistical interaction occurred (Table 2). Tropical grass cell walls are less digestible than cell walls of temperate grasses (Minson, 1990); however, grinding and pelleting usually decreases ruminal fibre digestibility because of shortened ruminal digesta residence time (Fahey *et al.* 1993).

Ruminal NH_3-N concentration was not significantly affected by grinding and pelleting but was greater ($P = 0{\cdot}09$) for RW than for B (Table 3), perhaps in large part because of the difference in forage N concentration. However, the difference in ruminal NH_3-N concentration was less than expected based simply on forage N concentration. Because a statistical interaction between grass source and physical form was not detected, perhaps synchrony of fermentation was not markedly changed by grinding and pelleting.

Proportions of a 24 h period spent standing and lying were not affected by diet (Table 3). Grinding and pelleting slightly increased eating time with B, but with RW a decrease occurred (interaction; $P = 0{\cdot}03$). Grinding and pelleting markedly decreased ($P < 0{\cdot}01$) time spent ruminating, which largely accounted for a substantial increase ($P < 0{\cdot}01$) in idle time.

Table 3. *Rumen fluid ammonia-nitrogen concentration and behaviour in wethers consuming bermudagrass or ryegrass–wheat coarsely chopped or ground and pelleted**

(Mean values and pooled standard error for four sheep per dietary group)

Variable	Bermudagrass		Ryegrass–wheat		SEM†	Statistical significance of effect of:‡
	Coarsely chopped	Ground and pelleted	Coarsely chopped	Ground and pelleted		
Ammonia-N (mmol/l)	3·7	3·7	6·0	4·2	0·75	g
Behaviour (fraction of 24 h)						
Standing	0·294	0·357	0·365	0·378	0·0349	
Lying	0·706	0·643	0·635	0·622	0·0349	
Eating	0·174	0·198	0·227	0·161	0·0173	I
Ruminating	0·424	0·323	0·383	0·281	0·0316	F
Idle	0·401	0·479	0·391	0·557	0·0268	F

* For details of diets and procedures, see Table 1 and pp. 770–772.

† Error df 12.

‡ g, grass source (bermudagrass *v.* ryegrass–wheat; $P < 0{\cdot}10$); F, grass form (coarsely chopped *v.* ground and pelleted; $P < 0{\cdot}05$); I, interaction between grass source and form ($P < 0{\cdot}05$).

Blood flow and oxygen

Portal and hepatic venous and hepatic arterial blood flows were not affected by diet (Table 4). O_2 consumption by the PDV was increased ($P = 0{\cdot}07$) by grinding and pelleting but was similar for B and RW diets; splanchnic bed O_2 consumption was greater ($P = 0{\cdot}07$) for ground and pelleted than for coarsely chopped grass; and hepatic O_2 consumption tended ($P = 0{\cdot}11$) to be greater for ground and pelleted than for coarsely chopped grass. Expressed on a daily basis and assuming 0·46 MJ heat energy produced per mol O_2 consumed (McLean, 1972), as a proportion of DEI, PDV and splanchnic heat energy production were greater for B than for RW, and a similar trend ($P = 0{\cdot}13$) in hepatic heat energy production occurred. The significance level of grass form effects for PDV, hepatic and splanchnic heat energy production as a proportion of DEI was 0·14.

That grass source and form were not statistically interactive in the ratio splanchnic bed heat energy production:DEI suggests that physical characteristics of forage affected by grinding and pelleting were not responsible for the higher ratio for B than for RW diets. Influences of factors other than DEI, or physiological workload, on splanchnic tissue heat production relative to DEI may be evidenced by a higher correlation between splanchnic tissue O_2 consumption and DM intake (r 0·63; $P = 0{\cdot}01$) than between splanchnic tissue O_2 consumption and DEI (r 0·53; $P = 0{\cdot}04$). However, results of this experiment do not allow identification of characteristics of B or physiological changes its consumption elicited that were responsible for greater splanchnic heat production:DEI compared with consumption of RW. Nonetheless, two factors that may have contributed to this difference involve gut digesta mass and eating time.

The 'girder' structure of tropical grass fragments, entailing plant tissues with protruding and jagged edges, leads to entanglement in the rumen digesta mat, which contributes to slow rumen digesta exit and high digesta mass (Wilson, 1993). In accordance, reticulo-rumen digesta mass has been shown to be greater for tropical than for temperate grass diets (Sun *et al.* 1994; Kouakou *et al.* 1995*a*,*b*). The proportion and integrity of arrangements of specific plant tissues presumably were not affected by grinding and pelleting in the present experiment (Fahey *et al.* 1993; Berger *et al.* 1994). Thus, grinding and pelleting may not have altered differences between grass sources in digesta mass. Digesta mass appears to have an impact on PDV energy consumption (Reynolds *et al.* 1991; Sun *et al.* 1994; Kouakou *et al.* 1995*b*) via expenditures for gut muscular contractions and in epithelial cell metabolic activity, with effects on the latter factor being much greater (Webster, 1980). In addition, effects of the nature of digesta in the gut, apart from its mass, on gut tissue energy use are plausible. Results of Rompala *et al.* (1988, 1990) provide some support for this possibility, as effects of dietary addition of inert bulky substances with constant DEI altered gastrointestinal tract tissue characteristics.

The second factor presumably contributing to the lower splanchnic tissue energy use:DEI ratio for B than for RW is the longer period of time spent eating relative to DEI. The relationship between eating time and PDV heat production encompasses muscular activities involved in prehension, mastication, swallowing and gut contractions and gut epithelial cell metabolism, although again, the largest contributor is metabolism by the gut epithelium (Kelly *et al.* 1989; Seal & Reynolds, 1993). How eating time may have interacted with differences in digesta characteristics and the relative importances of each factor in influencing PDV energy use in the present experiment are unclear. Other factors not measured that may have been involved in the different ratio for the grass sources include potential differences in microbial production and gastrointestinal tract concentrations and absorption of volatile fatty acids.

Table 4. *Whole-blood flow and oxygen and α-amino, urea and ammonia nitrogen measures in sheep consuming bermudagrass or ryegrass–wheat coarsely chopped or ground and pelleted**

(Mean values and pooled standard error for four sheep per dietary group)

Variable	Bermudagrass		Ryegrass–wheat		SEM†	Statistical significance of effect of:‡
	Coarsely chopped	Ground and pelleted	Coarsely chopped	Ground and pelleted		
Blood flow (litres/h)						
Portal vein	112	121	103	110	10·6	
Hepatic vein	127	147	124	131	12·0	
Hepatic artery	15	21	21	21	2·7	
Oxygen						
Whole-blood concentration (mmol/l)						
Portal vein	2·87	2·73	2·99	2·95	0·229	
Hepatic vein	2·38	2·24‖	2·41	2·32	0·244	
Artery	3·93	4·09	4·40	4·37	0·255	
Consumption (mmol/h)						
Portal-drained viscera	118	165	144	155	14·2	f
Hepatic	78	106	103	111	10·6	
Splanchnic	196	273	247	266	24·0	f
Heat energy production : digestible energy intake§						
Portal-drained viscera	0·225	0·188	0·163	0·128	0·0227	G
Hepatic	0·149	0·116	0·115	0·091	0·0180	
Splanchnic	0·374	0·300	0·278	0·219	0·0412	g
α-Amino-N						
Whole-blood concentration (mmol/l)						
Portal vein	4·27	4·91	4·73	5·62	0·296	g, F
Hepatic vein	4·14	5·02‖	4·55	5·44	0·303	F
Artery	4·16	4·80	4·49	5·36	0·286	F
Net flux (mmol/h)						
Portal-drained viscera	11·6	12·8	23·0	28·7	3·74	G
Hepatic	−15·2	−6·1‖	−17·0	−19·3	3·81	g
Splanchnic	−3·5	8·3‖	6·0	9·4	5·38	
Urea-N						
Whole-blood concentration (mmol/l)						
Portal vein	4·02	2·23	3·30	2·99	0·447	F
Hepatic vein	4·21	2·24‖	3·60	3·21	0·500	F
Artery	4·17	2·35	3·53	3·13	0·468	F
Net flux (mmol/h)						
Portal-drained viscera	−17·2	−14·7	−24·5	−15·0	4·11	
Hepatic	22·6	12·7‖	31·4	24·8	4·05	G, f
Splanchnic	5·3	−0·5‖	7·0	9·8	2·44	G
Ammonia-N						
Whole-blood concentration (mmol/l)						
Portal vein	0·500	0·531	0·588	0·584	0·0595	
Hepatic vein	0·366	0·462‖	0·405	0·487	0·0709	
Artery	0·388	0·479	0·433	0·502	0·0715	
Net flux (mmol/h)						
Portal-drained viscera	12·5	6·2	15·7	8·9	2·34	F
Hepatic	−15·2	−8·8‖	−19·3	−10·9	2·42	F
Splanchnic	−2·7	−2·6‖	−3·6	−2·0	1·32	

* For details of diets and procedures, see Table 1 and pp. 770–772.

† Error df for portal venous and arterial blood concentrations and portal-drained viscera net fluxes 12; error df for hepatic venous blood concentrations and hepatic and splanchnic net fluxes 11.

‡ G and g, grass source (bermudagrass *v.* ryegrass–wheat; $P < 0·05$ and $P < 0·10$ respectively); F and f, grass form (coarsely chopped *v.* ground and pelleted; $P < 0·05$ and $P < 0·10$ respectively).

§ Assuming 0·46 MJ heat energy per mol O_2 consumed.

‖ *n* 3.

Differences between grass sources in splanchnic tissue heat energy production relative to DEI were similar to results of previous experiments with *ad libitum* intake where differences were found to be due to factors other than DEI (Patil *et al.* 1995, 1996; Goetsch *et al.* 1996). Conversely, DEI as an index of physiological workload appears to be a relatively more important determinant of splanchnic tissue energy use with limited or restricted intake (Johnson *et al.* 1990). Perhaps metabolic activity more closely aligns with, and is markedly influenced by, physiological workload at different levels of restricted feed intake; whereas, with *ad libitum* intake of various diets, the degree of excess in metabolic machinery maintained relative to energy and nutrients absorbed decreases with increasing DEI and is relatively susceptible to influences of conditions apart from DEI.

Nitrogenous compounds

Release of AAN by the PDV was greater ($P < 0{\cdot}01$) for RW than for B (Table 4), which probably may be explained by greater microbial protein synthesis with greater DEI and digestible N intake for RW than for B. Possibly as a result of the difference between grass sources in PDV AAN release, hepatic uptake of AAN was greater ($P = 0{\cdot}07$) for RW, implying at least a slight excess of amino acids available to peripheral tissues relative to protein requirement. This is supported by greater ($P = 0{\cdot}03$) splanchnic UN release for RW than for B, suggesting that the quantity of amino acids available to peripheral tissues coincided more closely with the rate of protein synthesis supported by available energy from B than RW diets.

Grass form did not influence AAN net fluxes (Table 4), suggesting that microbial protein synthesis was not enhanced by grinding and pelleting or that intestinal availability of feed protein escaping ruminal digestion was depressed by grinding and pelleting. Concentrations of acid-detergent fibre-N, soluble N and insoluble available N in feedstuffs imply that grinding and pelleting did not appreciably change rumen outflow of intestinally available feed protein, and perhaps elicited a slight decrease. In support, PDV release and hepatic uptake of NH_3-N were lower ($P = 0{\cdot}02$ and $P = 0{\cdot}01$ respectively) for ground and pelleted than for coarsely chopped grass, indicating that rumen protein degradation was lessened by grinding and pelleting. Thus, grinding and pelleting did not appear to increase microbial protein synthesis. In accordance, grinding and pelleting has inconsistently altered microbial protein synthesis and growth efficiency (Fahey *et al.* 1993; Berger *et al.* 1994). However, other factors that could have been involved in these results include effects of grass form on the quantity of amino acids released by the PDV in peptides, accompanied by an underestimation of amino acid release with AAN as the index, and change in PDV metabolism of amino acids.

UN uptake by the PDV (Table 4) was not influenced by either grass source or form, which may relate to concurrent changes in DEI and digestible N intake. Hepatic UN release was greater for RW than for B ($P = 0{\cdot}03$) and for coarsely chopped than for ground and pelleted grass ($P = 0{\cdot}07$). Hepatic uptakes of both AAN and NH_3-N were correlated with UN hepatic release (r 0·71 and r 0·81 respectively; $P < 0{\cdot}01$). Even though not all NH_3-N and AAN taken up by the liver gives rise to UN, a regression of hepatic UN release on NH_3-N and AAN uptakes accounted for 74 % of variation, of which 64 and 36 % was attributable to uptakes of NH_3-N and AAN respectively. As a proportion of hepatic UN release, hepatic uptake of AAN was similar among treatments (0·65 (SE 0·078)), whereas hepatic NH_3-N uptake was greater ($P = 0{\cdot}09$) for B than for RW (0·83, 0·70, 0·61 and 0·45 for B-CC, B-GP, RW-CC and RW-GP respectively; SEM 0·123). Hence, NH_3-N may have contributed relatively more N to urea being released by the liver with B than RW diets.

This may relate both to the lower digestibility of B than of RW, which limited potential for rumen microbial incorporation of NH_3-N, and to presumably lower microbial protein production and subsequent intestinal absorption of amino acids with B. These results depict the importance of adequate rumen fermentable organic matter for capture of a high proportion of N in forage protein by rumen micro-organisms and impact of the rumen available N:organic matter ratio on N ultimately excreted as urea.

Glucose, propionate and lactate

Glucose net fluxes were not influenced by dietary treatment (Table 5). Therefore, it appears that PDV metabolism of glucose did not change with DEI as it varied with grass source and form. This is in contrast with relationships between DEI or metabolizable energy intake

Table 5. *Glucose, propionate and lactate measures in wethers consuming bermudagrass or ryegrass–wheat coarsely chopped or ground and pelleted**

(Mean values and pooled standard errors for four sheep per dietary group)

Variable	Bermudagrass		Ryegrass–wheat		SEM†	Statistical significance of effect of:‡
	Coarsely chopped	Ground and pelleted	Coarsely chopped	Ground and pelleted		
Glucose						
Plasma concentration (mmol/l)						
Portal vein	2·60	2·86	3·05	3·40	0·160	G, f
Hepatic vein	2·92	3·11§	3·40	3·70	0·172	G
Artery	2·71	2·89	3·14	3·51	0·156	G, f
Net flux (mmol/h)						
Portal-drained viscera	−10·3	−2·7	−8·3	−9·3	5·82	
Hepatic	30·4	19·2§	32·1	27·7	4·87	
Splanchnic	20·1	16·0§	23·8	18·4	5·04	
Propionate						
Whole-blood concentration (mmol/l)						
Portal vein	0·186	0·164	0·243	0·229	0·0426	
Hepatic vein	0·049	0·034§	0·056	0·038	0·0110	
Artery	0·037	0·027	0·044	0·028	0·0062	f
Net flux (mmol/h)						
Portal-drained viscera	16·5	17·6	21·6	23·2	5·63	
Hepatic	−15·1	−17·8§	−20·0	−22·2	6·25	
Splanchnic	1·4	1·2§	1·6	1·0	1·26	
Lactate						
Whole-blood concentration (mmol/l)						
Portal vein	0·45	0·65	0·56	0·65	0·075	f
Hepatic vein	0·33	0·46§	0·40	0·40	0·051	
Artery	0·34	0·48	0·45	0·42	0·059	
Net flux (mmol/h)						
Portal-drained viscera	11·2	19·7	11·2	25·3	5·45	f
Hepatic	−12·0	−22·6§	−17·4	−28·7	5·73	f
Splanchnic	−0·8	−8·0§	−6·2	−3·3	3·61	

* For details of diets and procedures, see Table 1 and pp. 770–772.

† Error df for portal venous and arterial blood concentrations and portal-drained viscera net fluxes 12; error df for hepatic venous blood concentrations and hepatic and splanchnic net fluxes 11.

‡ G, grass source (bermudagrass *v.* ryegrass-wheat; $P < 0·05$); f, grass form (coarsely chopped *v.* ground and pelleted; $P < 0·10$).

§ *n* 3.

and whole-body glucose turnover or hepatic production noted in other studies with limited intake (Brockman, 1993). This discrepancy may reflect a relatively small change in demand by the whole-body for glucose with differences in *ad libitum* intake of moderate- to low-quality forages compared with different levels of restricted intake. In accordance with no treatment effect on hepatic glucose release, propionate release by the PDV and hepatic uptake were not influenced by treatment. Lactate release by the PDV ($P = 0{\cdot}06$) and uptake by the liver ($P = 0{\cdot}08$) were greater for ground and pelleted than for coarsely chopped grass (Table 5). Reasons for these differences are not apparent. Lactate released by the PDV can arise from microbial production, which would not be expected to be appreciable with forage diets, and from epithelial cell metabolism of propionate and glucose. Because glucose uptake by the PDV was similar among diets, it is doubtful that change in its metabolism was responsible.

Summary

Results of this experiment indicate that splanchnic tissue energy metabolism relative to DEI differs between tropical and temperate grasses but is comparably enhanced by grinding and pelleting with similar increases in DEI. Possible factors responsible for such differences include effects of diet characteristics on gut digesta mass and thus on gut tissue mass, and energy used in heat-generating processes associated with eating. The absence of a statistical interaction between grass source and physical form suggests that physical characteristics of the forage influenced by grinding and pelleting (presumably primarily decreased particle size without marked change in the proportion or integrity of arrangements of specific plant tissues) were not responsible for differences between grass sources in splanchnic tissue energy consumption relative to DEI.

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