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The efficiency of energy utilization in growing cattle consuming fresh perennial ryegrass (*Lolium perenne* cv. Melle) or white clover (*Trifolium repens* cv. Blanca)

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1. Twenty Friesian steers (225 kg live weight) were fed on mid- (M) (June–July) and late- (L) (August–September) season crops of either fresh perennial ryegrass (*Lolium perenne* cv. Melle) (G) or white clover (*Trifolium repens* cv. Blanca) (C). Each of the forage diets was offered at three restricted planes of nutrition above maintenance to compare the effect of forage species on the efficiency of energy utilization. All diets were harvested daily from swards of regrowth forage of intended equivalent digestibility.

2. Faecal and urine excretions were measured for 7 and 5 d respectively, followed by two consecutive 24 h measurements of methane, carbon dioxide and oxygen exchange in open-circuit respiration chambers.

3. The apparent digestibility of the energy in perennial ryegrass (0·759) was marginally higher ($P < 0·01$) than that in white clover (0·748); the mid- and late-season forages were of similar ($P > 0·05$) digestibilities. Metabolizable energy (ME):digestible energy (DE) in diet G (0·837) was significantly ($P < 0·001$) different from that in diet C (0·812). The partition of energy losses when expressed as MJ/GJ gross energy intake (GEI) indicated that energy lost as methane was not significantly different ($P > 0·05$) either between forages (G 62·8, C 63·4) or between seasons (M 63·2, L 63·1). Energy excretion in urine was higher for cattle fed on diet C (77·5) compared with diet G (60·5) ($P < 0·001$). Heat production was similar ($P > 0·05$) between forages (G 480, C 478), but lower ($P < 0·01$) for L (471) compared with M(486). Energy retention (by difference) was lower ($P < 0·001$) for diet C (132) than G (156) and for M (138) than L (149) ($P < 0·05$).

4. Parallel-line analysis of unscaled ME intake (MEI) in relation to retained energy (RE; MJ/d) indicated that the efficiency of utilization (k_f) was similar ($P > 0·05$) between perennial ryegrass (0·42) and white clover (0·46). Linear extrapolation of the values to zero energy retention indicated that maintenance requirements of ME (E_m; MJ/d) were 23·3 for diet G and 28·8 for diet C. The extrapolated E_m when expressed in relation to a measured fasting heat production (FHP) of 22·8 (MJ/d) resulted in a derived efficiency of utilization of ME for maintenance (k_m) of 0·97 (G) and 0·79 (C), suggesting an underestimate of E_m for diet G.

5. Asymptotic exponential curves (representing the law of diminishing returns) were fitted to the unscaled values, MEI and RE (MJ/d), and extrapolated to zero energy retention and zero energy intake. The derived estimates of FHP (MJ/d) 18·0 (G) and 22·0 (C) were not significantly different ($P > 0·05$) from the observed value of 22·8 MJ/d. Using the measured FHP as additional data points, the exponential model accounted for significantly more variance ($P < 0·001$) compared with the linear regression method of analysis. Exponential analysis resulted in estimates of E_m (MJ/d) of 29·04 for diet G and 31·80 for C. The k_m for each forage was calculated, assuming linearity of response, as 0·78 (G) and 0·72 (C). The calculation of k_f at fixed positions on the exponential curve related to MEI (expressed as multiples of E_m) indicated that above 1·65 E_m, k_f was significantly higher for C than G ($P < 0·05$). With increasing plane of nutrition k_f declined from 0·53 to 0·29 (G) and 0·55 to 0·36 (C) over the MEI range measured during the experiment.

Perennial ryegrass (*Lolium perenne*; G) is the principal sown grass and makes a significant contribution to the energy and protein which ruminant livestock in the UK derive annually from forages. White clover (*Trifolium repens*; C) differs chemically in most respects from G and in particular has a higher protein and a lower cell wall content. Several studies have indicated that the productive potential of C is higher than that of grass of equivalent digestibility for both growth (Rae *et al.* 1963; Thomson, 1979) and lactation (Rogers *et al.* 1979; Gibb & Treacher, 1983; Thomson *et al.* 1985).

The improved performance of animals fed on C has been ascribed in part to a higher

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voluntary intake (Ulyatt *et al.* 1977), to an enhanced supply of absorbed protein (MacRae & Ulyatt, 1974; Ulyatt *et al.* 1980; Beever *et al.* 1985) and to an enhanced utilization of metabolizable energy (ME) for growth and fattening (Joyce & Newth, 1967; Rattray & Joyce, 1974).

The present work was undertaken as part of a programme to investigate the nutritive value of fresh grass and legume forages to identify and quantify the factors contributing to the improved animal production obtained by feeding C. The partition of energy loss was examined, including estimation of heat production by open-circuit calorimetry, to determine the efficiency of energy utilization by young cattle given both mid- (M) and late- (L) season cuts of either fresh G or C.

MATERIALS AND METHODS

Diets

Two forages: G (cv. Melle) and C (cv. Blanca) were harvested from swards which were 5 and 3 years old respectively. In early spring G received 60 kg nitrogen/ha of compound fertilizer (N–phosphorus–potassium; 20:10:10, w/w), and C received an equivalent amount of P and K, but no N was applied to this crop at any time throughout the season. The resulting primary growths of G and C were removed by mechanical harvesting in late May and mid-June respectively and the two fields were then appropriately divided into plots to allow successive 4 week (G) and 3 week (C) regrowths to be established, with the objective of harvesting forage from G and C of equivalent digestibility. Following each harvest the grass swards received an extra 60 kg N/ha. All swards were irrigated in an attempt to constrain soil moisture deficit.

Pre-experimental management of animals

Twenty-two 10-d-old Friesian male castrate calves (mean live weight (LW) 49 kg) were uniformly reared on milk-substitute to 6 weeks of age followed by hay and concentrates to 23 weeks of age. Between 23 and 26 weeks all calves were given a mixture of G and C (50:50, w/w) at a fixed level of intake of 26 g dry matter (DM)/kg LW. The LW range at 26 weeks of age was 170–230 kg (mean 190 kg).

At 18 weeks of age all animals were paired on the basis of LW and a provisional allocation made to either G or C treatments. Subsequently, within each group the animals were blocked according to LW, and randomly allocated to three levels of feeding. Between weeks 18 and 23 all animals were allowed access to metabolism cages and the respiration chambers so that they could become accustomed to the procedures before the start of experimental measurements. At week 26 the experimental diets were introduced at the designated feeding levels to all animals except the two intended for measurement of fasting heat production (FHP) which were maintained on a G and C mixture at the median level of feeding. All animals were housed on partially slatted floor pens except during the faecal and urine collection periods.

Experimental design

The experiment was conducted over a period of 106 d as part of a production slaughter balance experiment. Due to the extended feeding period required for the comparative slaughter study, the two forage species G and C could be considered as mid-season (M), given during June and July, days 14–52 of the experiment (MG and MC respectively); and late season (L), given during August and September, days 53–91 of the experiment (LG and LC respectively). Each crop was offered at three levels of feeding: 20, 23 and 26 g DM/kg LW (levels 1, 2 and 3 respectively). A total of four animals were allocated to level 1 and three to each of levels 2 and 3, the remaining two animals were retained separately for subsequent estimates of FHP. No further reallocation of animals was made for the duration of the experiment and all animals were used for the measurement of respiratory exchange with the exception of one animal on forage C which died from bloat. Two respiration chambers were available, consequently faecal and urine balance measurements were undertaken immediately before respiratory exchange in a sequential order appropriate to the age of the regrowth herbage on the plots and the designated M and L seasons.

Experimental procedures

The two forages were harvested separately each morning at 07.30 hours. The crops were cut using a rotary drum mower and the cut material was then immediately harvested without chopping using a direct pick-up forage wagon with the stationary cutting knives removed. After delivery to the animal house a 5 kg representative sample of each forage was taken and used to provide two 100 g samples for rapid DM determination using a modified microwave oven. During feed weighing, representative bulked samples of each forage were taken and subsequently four 500 g samples were prepared for DM determination by oven drying at 100° for 24 h. A further 1 kg subsample of each forage was immediately frozen for subsequent chemical analysis.

Daily fresh weight allowances were calculated on the basis of the initial rapid estimates of DM content and the appropriate LW of the animals. The forages were offered to the animals in two equal amounts at 09.30 and 16.00 hours. The forage for the afternoon feeding was held at 2° in a cold room. The animals on diet C received an oral dose (5 ml at each feed) of Poloxalene (Smith, Kline & French, Welwyn Garden City, Herts.) to control bloat. Feed refusals, where they occurred, were removed daily before the 09.30 hours feeding and dried at 100° for 24 h to determine DM content.

LW were recorded weekly on two consecutive days between 07.30 and 08.30 hours, with the exception of the animals on faecal and urine balance and respiratory exchange measurements, and food allowance was adjusted weekly according to the predetermined levels of feeding. No adjustments to food allowance were made during balance and calorimetric measurements.

Faeces and urine were collected for seven and five consecutive days respectively, before entry into the respiration chambers, using the procedures decribed by Cammell (1977). The animals were then placed in open-circuit respiration chambers for 3 d, comprising day 1 for acclimatization and days 2 and 3 for consecutive 24 h measurements of respiratory exchange. Respiration measurements were conducted as described by Cammell *et al.* (1981) with the exception that the chambers used were constructed of double-skin steel insulated panels and had an internal volume of 15 m^3. Additionally each chamber had a recirculatory air conditioning system to provide environmental control within a temperature range of $18\pm2°$ and relative humidity (RH) of $60\pm10\%$. Gaseous composition of the in- and out-going air from the respiration chambers was measured using dual-channel infra-red (Analytical Development Co. Ltd, Hoddesdon, Herts.) and paramagnetic analysers (Taylor Instrument Analytics Ltd, Crowborough, Sussex). Measurement of the volume of gases leaving each chamber and the method of sampling was as previously described by Cammell *et al.* (1981). Measurements of FHP were determined on days 1–4, 51–54 and 103–106 of the experiment, using procedures described by Blaxter (1962), with the exception that total length of fast was 96 h and included two consecutive days of measurement between 48 and 96 h.

Preparation and analysis of samples

All samples of feed taken at the time of weighing were freeze-dried and ground through a small laboratory mill. For each animal the faeces voided daily were mixed and a representative sample comprising 10% of total daily fresh weight was withdrawn and accumulated for 7 d in a cold store at −5°. The bulked samples were thoroughly mixed after thawing and part (4 × 500 g) was dried at 100° for 48 h to determine DM content and a further portion (500 g) was freeze-dried to provide a sample, after grinding, for chemical analysis. Samples of feed and faeces were analysed for organic matter (ashing to 550° overnight), total N (micro-Kjeldahl) and gross energy (GE; adiabatic calorimetry) contents. Feed samples were further analysed for in vitro organic matter digestibility in DM (DOMD) (Tilley & Terry, 1963) and buffer-insoluble N content (Siddons & Paradine, 1981).

Acidified urine samples were accumulated for 5 d on a fresh basis (1% of total daily output) and urinary N content was determined by micro-Kjeldahl, using fresh samples. Urinary energy contents were estimated after the samples had been dried under reduced pressure in a rotary evaporator at 40° followed by resolubilization in a minimal quantity of distilled water to permit total combustion (after freeze-drying in a thin-walled polyethylene container) in an adiabatic bomb calorimeter (R. A. Terry, personal communication).

Calculations

The sequential measurements of faecal and urinary output during the balance trials and the succeeding measurements of respiratory exchange by open-circuit calorimetry were associated with small changes in the composition of both the fresh forages. The consequent effects on faecal (FE) and urinary energy (UE) output necessitated a method of estimation for the days of respiratory exchange.

The best relation for the prediction of FE output was obtained from a multiple regression analysis of the FE losses during balance measurements incorporating GE intake (GEI) and DOMD. UE output was similarly predicted using UE losses during balance measurements, GEI, DOMD and N intake (NI). The regressions for season within each forage were derived, tested for differences in slope and intercept and combined where appropriate. These estimates were then used together with the observed values for methane production to calculate ME content of the diets and the ME intake (MEI).

Heat production (HP) was calculated according to Brouwer (1965), from the observed values for methane, oxygen and carbon dioxide exchange and derived urinary N excretion applicable to NI during the days of respiratory exchange. This latter relation was determined from a regression of all observed values for urinary N output and NI. Retained energy (RE) was calculated as the difference between MEI and HP.

Statistical analysis

Results for the chemical composition, intake, digestibility coefficients (as measured), the partition of energy losses between faeces and urine (derived from eqns (3) and (4), p. 674), methane, heat output and energy retention were analysed as a 2 × 2 factorial design (i.e. two forages G and C, two seasons M and L) and adjusted for level of feeding using a regression analysis of variance.

Two methods of analysis were used to examine the data for RE and MEI: linear regression and exponential curve analysis. The exponential method followed the general model:

$$\mathrm{RE} = \mathrm{P}_3[1-\exp(-\mathrm{P}_1(\mathrm{MEI}-\mathrm{P}_2))], \tag{1}$$

where P_1 is the curvature or specific rate, P_2 is equivalent to E_m, P_3 is the asymptote and $\mathrm{P}_3[1-\exp(\mathrm{P}_1\,\mathrm{P}_2)]$ is the estimation of FHP (F2). Differentiation of eqn (1) with respect to MEI allows calculation of the efficiency of utilization, k_f, at any value of MEI, i.e. $k_\mathrm{f} = \mathrm{d(RE)/d\,(MEI)}$ thus:

$$k_\mathrm{f} = \mathrm{P}_1\,\mathrm{P}_3\exp[-\mathrm{P}_1(\mathrm{MEI}-\mathrm{P}_2)]. \tag{2}$$

The relations used to predict FE and UE were examined using mean square prediction error (MSPE) analysis (Neal *et al.* 1984) and the Bootstrap method (Efron, 1979).

Table 1. *The chemical composition of the mid- (M) and late- (L) season cuts of fresh perennial ryegrass* (Lolium perenne *cv. Melle) and white clover* (Trifolium repens *cv. Blanca)*

(Values expressed as g/kg dry matter (DM) unless otherwise stated)

	Perennial ryegrass		White clover			Statistical significance of effect of:	
	M	L	M	L	SEM	Forage	Season
DM (g/kg)	185·7	162·7	150·8	126·8	3·22	***	***
Ash	96·8	97·2	94·5	101·9	1·59	NS	**
Nitrogen	25·7	29·9	42·9	44·8	0·58	***	***
Insoluble N	22·0	25·9	34·8	37·8	0·50	***	***
Gross energy:							
MJ/kg DM	18·0	18·6	18·8	19·1	0·05	***	***
MJ/kg OM	20·0	20·6	20·8	21·2	0·06	***	***
In vitro DOMD†	0·702	0·687	0·681	0·675	0·005	***	***
In vitro DOMD‡	0·697	0·683	0·672	0·676	0·005	***	***

OM, organic matter; DOMD, digestibility of organic matter in dry matter; NS, not significant.
** $P < 0·01$, *** $P < 0·001$.
† Mean value during faecal and urine balance measurements.
‡ Mean value during respiratory exchange measurements.

RESULTS

The chemical composition of the diets is presented in Table 1.

Significant differences were found between the forages G and C ($P < 0·001$) and between the seasons M and L ($P < 0·01$) in all chemical constituents with the exception of the ash content. The results demonstrate the inherent differences in composition of the two forages. The N content of C was higher than that in G; also GE content, both on a DM and organic matter basis, was higher than that of the grass. The in vitro DOMD results are given as weighted means for each forage season and represent the mean values observed during the consecutive periods of faecal/urine balance and respiratory exchange measurements. The values for in vitro DOMD for the days of respiratory exchange were not significantly different from those for faecal/urine balance, except for the MC values ($P < 0·001$). The difference between the forages for the days of respiratory exchange (G 0·690, C 0·674) was primarily due to the difference between the M forages (G 0·697, C 0·672), as a result of water stress which appeared to induce earlier flowering of the C crop. This resulted in the harvested material containing a higher proportion of mature inflorescence and their supporting stems which had a lower in vitro digestibility than the leaf and petiole components (Gibb & Treacher, 1983). The significant ($P < 0·01$) seasonal effect in the ash content was associated with a reduction in the cutting height of the forages and the consequent increase in soil contamination especially as seen on diet LC. There was a significant ($P < 0·001$) increase in the N contents of both forages from M- to L-season cuts. Chemical analysis of fibre was restricted to feed samples from the comparative slaughter study and the overall values for G and C respectively (g/kg DM) for neutral-detergent fibre were 426·7 and 216·1, acid-detergent fibre 266·2 and 210·9, lignin 26·7 and 38·2, pectin 7·8 and 39·9. The values were significantly different ($P < 0·001$) between G and C.

The apparent digestibility of the organic matter (OMD), N (ADN) and GE (ADE) at the three restricted levels of feeding are given in Table 2. The ADN values of G were significantly ($P < 0·001$) lower, and OMD and ADE values significantly ($P < 0·05$ and 0·01 respectively) higher than C. This latter effect was primarily due to differences between the

Table 2. *Coefficients of apparent digestibility of the organic matter, nitrogen and energy in mid- (M) and late- (L) season cuts of fresh perennial ryegrass* (Lolium perenne *cv. Melle*) *and white clover* (Trifolium repens *cv, Blanca*) *given to Friesian steers at three restricted levels of feeding*

	Level of feeding†	Perennial ryegrass		White clover			Statistical significance of effect of:		
		M	L	M	L	SEM	Forage	Season	Level
Organic matter	1	0·812	0·811	0·789	0·804	0·0107	*	NS	*
	2	0·805	0·798	0·798	0·799				
	3	0·806	0·791	0·761	0·777				
N	1	0·681	0·766	0·776	0·811	0·0173	***	***	NS
	2	0·693	0·754	0·789	0·801				
	3	0·690	0·711	0·771	0·798				
Energy	1	0·763	0·768	0·748	0·759	0·0066	**	NS	**
	2	0·763	0·753	0·748	0·758				
	3	0·755	0·749	0·715	0·758				

NS, not significant. * $P < 0{\cdot}05$, ** $P < 0{\cdot}01$, *** $P < 0{\cdot}001$. † For details, see p. 670.

M forages where early flowering induced by water stress was associated with declining in vitro digestibility of the MC forage. Significant ($P < 0{\cdot}001$) differences due to season were restricted to ADN, where L crops were higher than M. Significant differences ($P < 0{\cdot}05$ and 0·01 respectively) due to level of feeding were apparent for both OMD and ADE.

Predictive relations for FE and UE excretion from forages G and C are given in Table 3. These were derived as previously described from the pooled observed values from balance measurements. The use of these individual forage relations did not significantly improve ($P > 0{\cdot}05$) the variance accounted for when compared with the combined G and C overall relations, eqns (3) and (4):

$$\text{FE} = 0{\cdot}2473\ \text{GEI} - 44{\cdot}7908\ \text{DOMD} + 30{\cdot}3758\ (r\ 0{\cdot}861,\ \text{residual SD (RSD)}\ 1{\cdot}45928), \tag{3}$$

$$\text{UE} = 0{\cdot}0257\ \text{GEI} - 3{\cdot}1336\ \text{DOMD} + 0{\cdot}0223\ \text{NI} + 2{\cdot}0974\ (r\ 0{\cdot}850,\ \text{RSD}\ 0{\cdot}62883), \tag{4}$$

where FE, UE and GEI are expressed as MJ/d and NI as g/d.

The possibility of significant differences in the spread of predicted values of either FE or UE from the overall relations when compared with individual relations for G and C, were examined using MSPE analysis and the Bootstrap method.

MSPE results showed non-significant biases (individual – overall) ($P > 0{\cdot}05$) for both FE and UE predictions. For G and C respectively, the bias in the prediction of FE (MJ/d) was −0·682 (SE 0·3806), −0·122 (SE 0·1202) and for UE (MJ/d) +0·235 (SE 0·3650), −0·115 (SE 0·1293).

The Bootstrap method also indicated no significant differences ($P > 0{\cdot}05$) between the predictive relations. The coefficients of variation for eqn (3) were (G) 8·674, (C) 8·674 which were lower than the individual forage relations (Table 3) (G) 9·464, (C) 8·787. The coefficients of variation for eqn (4) were also lower (G) 8·844, (C) 4·917 than the individual relations (G) 13·755, (C) 5·454.

As a result of these statistical analyses the overall relations as given in eqns (3) and (4) were used to predict FE and UE as presented in Table 4.

During the days of respiratory exchange, the measured GEI, methane and heat energy output (MJ/GJ GEI), together with FE and UE outputs derived from eqns (3) and (4), and LW derived from the relation of LW *v.* time-period of respiratory exchange have been

Table 3. *The regression equations relating (a) energy loss (Y; MJ/d) in faeces to gross energy intake (GEI; MJ/d) and in vitro digestibility of organic matter in dry matter (DOMD), and (b) energy loss (Y; MJ/d) in urine to GEI, in vitro DOMD and nitrogen intake (NI; g/d) for Friesian steers fed on fresh perennial ryegrass* (Lolium perenne *cv. Melle) and white clover* (Trifolium repens *cv. Blanca)*

(The values are combined for mid- and late season and three levels of feeding)

	Perennial ryegrass	White clover
(*a*) Faeces	$Y = 0{\cdot}2679$ GEI $- 13{\cdot}5128$ DOMD $+6{\cdot}9365$ r 0·865, RSD 1·31957	$Y = 0{\cdot}2447$ GEI $- 55{\cdot}4003$ DOMD $+37{\cdot}6281$ r 0·866, RSD 1·67575
(*b*) Urine	$Y = 0{\cdot}0008$ GEI $+ 28{\cdot}3934$ DOMD $+0{\cdot}0471$ NI$-20{\cdot}7221$ r 0·738, RSD 0·77576	$Y = 0{\cdot}0509$ GEI $+ 1{\cdot}6273$ DOMD $+0{\cdot}0082$ NI$-0{\cdot}3892$ r 0·896, RSD 0·43521

RSD, residual SD.

Table 4. *The live weight (kg), gross energy intake (GEI; MJ/d) and the loss of energy in faeces (eqn (3))†, urine (eqn (4))†, methane and heat and the energy retention (MJ/GJ GEI) during the days of respiratory exchange by Friesian steers fed mid- (M) and late- (L) season cuts of fresh perennial ryegrass* (Lolium perenne *cv. Melle) and white clover* (Trifolium repens *cv. Blanca)*

(Values are presented as means of three levels of feeding)

	Perennial ryegrass		White clover			Statistical significance of effect of:	
	M	L	M	L	SEM	Forage	Season
Live wt	229	258	217	249	3·3	**	***
GEI	85·6	100·2	84·4	101·6	1·34	NS	***
Energy loss as:							
Faeces	236·9	244·3	254·3	245·9	2·91	***	NS
Urine	57·5	63·4	76·6	78·4	0·70	***	*
Methane	64·2	61·5	62·1	64·8	0·62	NS	NS
Heat	483·7	475·8	488·3	467·1	3·80	NS	**
Energy retention	157·4	154·9	119·4	143·8	4·48	***	*

NS, not significant. * $P < 0{\cdot}05$, ** $P < 0{\cdot}01$, *** $P < 0{\cdot}001$. † For details, see p. 674.

pooled across levels and are presented in Table 4. GEI was similar for both forages, but was significantly higher ($P < 0{\cdot}001$) for the L crops, although scaling for LW removed this effect. The mean values of FE and UE (MJ/GJ GEI) were higher ($P < 0{\cdot}001$) for C (250, 78) than G (241, 60), but neither forage nor season had any significant effect on methane energy output (MJ/GJ GEI).

The ME contents (MJ/kg DM) of the forages were obtained by deducting the FE and UE outputs, calculated from eqns (3) and (4), and the methane energy output from GEI (observed), and dividing by DM intake. The values were 11·98 and 11·60 for diets MG and LG respectively and 11·59 and 11·53 (SE 0·145) for MC and LC. There was a significant ($P < 0{\cdot}05$) difference between forages but no effect due to season ($P > 0{\cdot}05$).

ME:DE of the forages were 0·840 and 0·835 for MG and LG, 0·814 and 0·810 for MC

Table 5. (*a*) *The estimated coefficients relating to the partition of the metabolizable energy of perennial ryegrass* (Lolium perenne *cv. Melle*) *and white clover* (Trifolium repens *cv. Blanca*) *according to eqn* (*1*)†, *and* (*b*) *the predicted efficiency of utilization* (k_f) *according to eqn* (*2*)† *at several levels of metabolizable energy intake* (*MJ/d*)

	Perennial ryegrass		White clover		Statistical significance
		SEM		SEM	
(a) Parameter					
P_1 ($\times 10^{-3}$)	15·12	3·280	10·61	2·080	—
P_2	29·04	1·407	31·79	0·832	—
P_3	41·40	8·198	56·73	10·365	—
F_2	22·83	2·703	22·77	2·627	—
(b) Metabolizable energy intake					
40	0·530	0·0152	0·552	0·0222	NS
50	0·456	0·0064	0·496	0·0193	*
60	0·392	0·0040	0·446	0·0166	*
70	0·337	0·0091	0·401	0·0142	*
80	0·289	0·0139	0·361	0·0121	*

NS, not significant. * $P < 0.05$. † For details see p. 672.

and LC respectively. There was a significant ($P < 0.001$) difference between forages and a small but significant ($P < 0.05$) effect of season. Heat production (MJ/GJ GEI) was not significantly different between the forages; there was, however, a significant ($P < 0.01$) effect of season which was due primarily to the lower value recorded on diet LC. Energy retention (MJ/GJ GEI) was significantly affected by forage (G 156, C 132; $P < 0.001$) and season (M 138, L 149; $P < 0.05$), resulting from the low value (119) measured on the animals receiving diet MC due to higher FE and heat energy outputs (MJ/GJ GEI). The linear relations of RE on MEI (MJ/d) were:

$$\text{G: RE} = 0.4169\ \text{MEI} - 9.7010 \quad (r\ 0.902,\ \text{RSD}\ 1.636), \qquad (5)$$

$$\text{C: RE} = 0.4616\ \text{MEI} - 13.2995\ (r\ 0.964,\ \text{RSD}\ 1.451). \qquad (6)$$

No significant differences were found between forages although a small effect of season was observed. Scaling RE and MEI values by metabolic LW ($\text{LW}^{0.75}$) did not significantly improve the variance accounted for by the linear relations of the unscaled values. Linear extrapolation of eqns (5) and (6) indicated maintenance requirements (E_m) (MJ/d) at zero energy retention of G 23·3 and C 28·8. The measured mean value for FHP was 22·8 MJ/d. This value in relation to linear estimates of E_m for G would imply an efficiency of utilization of ME for maintenance, k_m, of 0·97, suggesting an underestimate of E_m.

The unscaled RE and MEI values were applied to the exponential model (eqn (1)) excluding the measured value of FHP. This resulted in estimates of FHP of G 18·0 and C 22·0 MJ/d, which were not significantly different either between forages or from the mean measured value of 22·8. Measured FHP was then used as an additional data point and the model re-run without constraining the curve through measured FHP. The unscaled RE and MEI values and the derived curve shown in Fig. 1 were used to obtain the parameters and predictions described in Table 5. The variance accounted for was significantly ($P < 0.001$) improved in comparison with the linear models (eqns (5) and (6)).

Parameter P_1 (eqn (1)) represents the rate of decline of k_f with increasing MEI. Fitting a common P_1 to diets G and C resulted in a significant increase ($P < 0.05$) in residual error variance, therefore separate curves were used for each forage. P_2 estimates the values for

E_m (29·04 and 31·80 (MJ/d) for G and C respectively) which were significantly ($P < 0·05$) different. The asymptote (P_3) represents the maximal potential energy retention for the forages. F_2 represents FHP: G 22·83, C 22·77 MJ/d. The k_m values derived from FHP and E_m, assuming linearity of response, were in close agreement with expected values for forage diets of similar metabolizability G 0·78, C 0·72 (Agricultural Research Council, 1980). The effect of the differences in the above parameters (P_1, P_2, P_3) is reflected in the derived k_f values at several levels of MEI. When calculated as multiples of E_m, significant differences ($P < 0·05$) due to forage species were apparent only above 1·65 E_m or 50 MJ MEI/d.

DISCUSSION

The objective of the present experiment was to evaluate the efficiency of energy utilization in growing cattle consuming either fresh G or C as pasture species. Due to the lack of appropriate techniques to measure accurately the ME intake of grazing animals, the experiment was conducted indoors under controlled conditions, using open-circuit respiration calorimetry.

The grass and legume forages, harvested daily in the long form, were also given in a related growth and tissue retention experiment (Thomson *et al.* 1983), using the same cattle, and also in a digestion and metabolism study (Cammell *et al.* 1983). The results of this study and the related comparative slaughter experiment permit a direct comparison between two different techniques for the measurement of RE and k_f. These will be discussed in a subsequent paper.

Current methods of analysis of energy balance measurements by respiration calorimetry have embraced the main conventions of separate linear analysis of negative (k_m) and positive (k_f) energy balance, with the derivation of k_f restrained to measurements between zero energy retention and twice maintenance level of feeding.

The results from this experiment were initially analysed according to the previously mentioned conventions, expressing the nutritive value of each forage as the linear response in RE per unit increase in ME intake. Overall estimates of the values (unscaled for $LW^{0·75}$) gave predicted values for k_f of G 0·42 and C 0·46 which were not significantly different. Scaling the values using $LW^{0·75}$ did not either significantly alter the estimated k_f or account for more of the variation. Extrapolation of the unscaled linear values to zero energy retention gave estimated values for E_m of G 23·3 and C 28·8 MJ ME/d, equivalent to 378 and 483 kJ ME/kg $LW^{0·75}$ per d for diets G and C respectively. The value derived for diet C was comparable to those obtained by Brierem (1953) and Van Es (1961) for growing cattle, but the value obtained for diet G was approximately 20% lower than would have been predicted on the basis of Agricultural Research Council (1980).

The measurement of FHP in the present study extended the range of values and permitted the calculation of k_m using the E_m as derived previously. This gave a value of 0·79 for diet C and 0·98 for diet G. This latter value was considered to be unacceptable in relation to values which have been quoted for diets of similar metabolizability (Agricultural Research Council, 1980).

Previously reported studies have demonstrated that the law of diminishing returns applies to the responses in energy retention with increasing plane of nutrition (Blaxter & Graham, 1955; Blaxter & Boyne, 1970, 1978; Agricultural Research Council, 1980). Alternative analysis of the values was undertaken using an asymptotic exponential model (Fig. 1 and Table 5), similar to the methods of analysis previously reported by Blaxter & Boyne (1978). The analysis enabled the values for MEI and RE to be incorporated with the predicted and measured values for FHP (unforced curve) and this was found to account for a greater proportion of the variance than the linear method. Additionally, it gave estimates of FHP

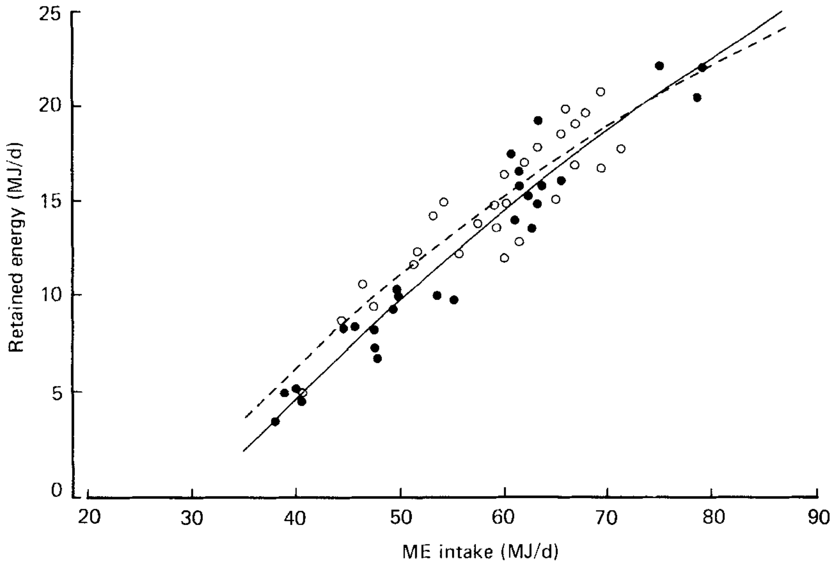

Fig. 1. The relation between retained energy (○, ●) and metabolizable energy (ME) intake (– – –, ——) (MJ/d) for fresh perennial ryegrass (*Lolium perenne* cv. Melle) (○, - - -) and white clover (*Trifolium repens* cv. Blanca) (●, ——) given to Friesian steers. Each point represents an individual daily observation. The overall forage relations are calculated according to eqn (1) (see p. 672).

(22·8 and 22·7 MJ/d for G and C respectively) which agreed both with the measured values and those previously reported by Vercoe & Frisch (1974), Webster *et al.* (1974) and Webster (1978) for growing cattle of similar age and LW. The estimated values of E_m were 29·0 and 31·8 MJ ME/d for G and C respectively. These were then used in conjunction with estimated FHP and by assuming linearity of response, values for k_m of G 0·79 and C 0·72 were derived which were found to be closer to theoretical expectations (Agricultural Research Council, 1980).

The scaled values ($LW^{0.75}$) were similarly analysed but did not account for a significantly greater proportion of variance than the unscaled exponential analysis.

The derivation of values for E_m in the present study required interpolation between recorded values at zero energy intake and levels of MEI above maintenance. Therefore, caution must be applied until further data sets are available close to and below zero energy retention. However, the constraints described by Webster (1978) indicate the difficulty inherent in any measurement of 'true' maintenance requirement for the growing animal.

With respect to the overall changes in RE with increments of MEI, the analysis of unscaled values (Table 5) indicated no significant differences between forage species. The divergence of the curves at higher increments of MEI, however, indicated a potential difference in RE and k_f. Parallel curve analysis showed that the curves were significantly different, thus permitting examination of differences between the parameters RE and calculated k_f (eqn (2)) at given points on the curve in relation to MEI. In this respect, a significant between-forage difference was indicated with the rate of decline in RE being greater for diet G compared with diet C at increasing levels of MEI, which in turn accounted for the higher estimates of theoretical potential RE (parameter P_3, Table 5) obtained on diet C compared with G. Estimates of k_f (eqn (2)) were calculated from each forage curve at ascending increments of MEI which were calculated as multiples of an E_m value of 30·42 MJ ME/d (derived from the mean of diets G and C). This indicated that for a

240 kg LW steer, when ME intakes were in excess of 1·65 E_m, significant differences in k_f were apparent between diets G and C (C > G).

The apparently higher gross efficiency of ME utilization on diet G, whilst not significantly different from diet C at levels of intake below 1·65 E_m, may result from differences in rumen fermentation patterns and changes in the proportions of energy yielding substrates absorbed (Beever *et al.* 1985).

Evidence of seasonal differences in k_f have been reported by Corbett *et al.* (1966) and Lonsdale & Tayler (1971). Forage season effects were not specifically examined in the present study but owing to the extended feeding period required for the comparative slaughter technique, the forages could be considered as M- and L-season crops.

Exponential analysis of the data for effects of season were restricted by the limited number of data sets and the degree of interpolation required to incorporate FHP. Accordingly, the analysis was restricted to conventional linear methods within the limited range of MEI. The analysis revealed that both MG and MC had higher values for k_f (G 0·51, C 0·54) than LG and LC (G 0·42, C 0·42). However, the derivation of these values was associated with increased statistical errors and accounted for a lower proportion of variance compared with either linear or exponential analysis of the combined data range for each forage species.

The results of the experiment are in agreement with those of Rattray & Joyce (1974) and confirm that C is potentially superior to G in terms of energy retention per unit MEI, but only at levels of feeding in excess of 1·65 E_m/d in this experiment. The theoretical potential, in terms of RE, would appear greater for C than for G, suggesting that nutrient availability was likely to limit first retention on diet G.

The reasons for differences between RE and k_f, observed for the two forages, require additional knowledge concerning the nature and quantity of nutrients absorbed after digestion and the effect of nutrient interaction and hormonal status on nutrient utilization. Evidence relating to fat and protein tissue deposition in the animals used in the present study will be presented in a subsequent paper.

The results of the present study clearly demonstrate that the conclusions which can be drawn will be markedly influenced by the mathematical model adopted to describe the data. In the present study, acceptance of an exponential model was necessary to reconcile fully the data but was not intended to provide unequivocal proof that the relation between MEI and RE is best described by an exponential function. However, this form of analysis appears biologically credible and some support for this approach has been previously presented by Blaxter & Boyne (1978) and more recently by Gill *et al.* (1984). The degree of interpolation required in the present study emphasizes the requirement for respiratory exchange measurements at additional levels of feeding in future experiments.

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REFERENCES

Agricultural Research Council (1980). *The Nutrient Requirements of Farm Livestock* no. 2. *Ruminants.* Farnham Royal: Commonwealth Agricultural Bureaux.

Beever, D. E., Thomson, D. J., Ulyatt, M. J., Cammell, S. B., Austin, A. R. & Spooner, M. C. (1985). *British Journal of Nutrition* **54**, 763–775.

Blaxter, K. L. (1962). *The Energy Metabolism of Ruminants*. London: Hutchinson.

Blaxter, K. L. & Boyne, A. W. (1970). In *Energy Metabolism of Farm Animals*, European Association for Animal Production Publication no. 13, pp. 9–13 [A. Schurch and C. Wenk, editors]. Vitznau, Switzerland; Juris Verlagzurich.

Blaxter, K. L. & Boyne, A. W. (1978). *Journal of Agricultural Science, Cambridge* **90**, 47–68.

Blaxter, K. L. & Graham, N. McC. (1955). *Journal of Agricultural Science, Cambridge* **46**, 292.

Brierem, K. (1953). *Tid Sskrift For Det Norske Landbruk* **60**, 25.

Brouwer, E. (1965). In *Energy Metabolism*, European Association for Animal Production Publication no. 11, pp. 441–443 [K. L. Blaxter, editor]. London & New York: Academic Press.

Cammell, S. B. (1977). *Technical Report* no. 24. Hurley: Grassland Research Institute.

Cammell, S. B., Beever, D. E., Skelton, K. V. & Spooner, M. C. (1981). *Laboratory Practice* **30**, 115–119.

Cammell, S. B., Beever, D. E., Thomson, D. J., Austin, A. R., Losada, H. R., Evans, R. T., Spooner, M. C. & Terry, R. A. (1983). *Animal Production* **36**, 501.

Corbett, J. L., Langlands, J. P., McDonald, I. & Pullar, J. D. (1966). *Animal Production* **8**, 13–27.

Efron, B. (1979). *Annals of Statistics* **7**, 1–26.

Gibb, M. J. & Treacher, T. T. (1983). *Animal Production* **37**, 433–440.

Gill, E. M., Black, J. L., Thornley, J. H. M., Oldham, J. D. & Beever, D. E. (1984). *British Journal of Nutrition* **52**, 621–649.

Joyce, J. P. & Newth, R. P. (1967). *Proceedings of the New Zealand Society of Animal Production* **27**, 166–180.

Lonsdale, C. R. & Tayler, J. C. (1971). *Animal Production* **13**, 384.

MacRae, J. C. & Ulyatt, M. J. (1974). *Journal of Agricultural Science, Cambridge* **82**, 309–319.

Neal, H. D. St. C., Thomas, C. & Cobby, J. M. (1984). *Journal of Agricultural Science* **103**, 1–10.

Rae, A. J., Brougham, B. W., Glenday, A. C. & Butler, G. W. (1963). *Journal of Agricultural Science, Cambridge* **61**, 187–190.

Rattray, P. V. & Joyce, J. P. (1974). *New Zealand Journal of Agricultural Research* **17**, 401–408.

Rogers, G. L., Porter, R. H. D. & Robinson, I. (1979). *Dairy Production Research Report*, pp. 59–60. Victoria, Australia: Department of Agriculture, Division of Animal Research.

Siddons, R. C. & Paradine, J. (1981). *Journal of the Science of Food and Agriculture* **32**, 973–981.

Thomson, D. J. (1979). In *Changes in Sward Composition and Productivity*, British Grassland Society, Occasional Symposium No. 10, pp. 101–109 [A. H. Charles and R. J. Haggar, editors]. York: British Grassland Society.

Thomson, D. J., Beever, D. E., Haines, J. J., Cammell, S. B., Evans, R. T., Dhanoa, M. S. & Austin, A. R. (1985). *Journal of Dairy Research* **52**, 17–31.

Thomson, D. J., Haines, M. J., Austin, A. R., Cammell, S. B., Beever, D. E., Dhanoa, M. S. & Barnes, R. L. (1983). *Animal Production* **36**, 501.

Tilley, J. M. A. & Terry, R. A. (1963). *Journal of the British Grassland Society* **18**, 104–111.

Ulyatt, M. J., Beever, D. E., Thomson, D. J., Evans, R. T. & Haines, M. J. (1980). *Proceedings of the Nutrition Society* **39**, 67A.

Ulyatt, M. J., Lancashire, J. A. & Jones, W. R. (1977). *Proceedings of the New Zealand Grassland Association* **38**, 107–118.

Van Es, A. J. H. (1961). *Verslagen van Landbouwkundige Onderzoekingen* **67**, 5.

Vercoe, J. E. & Frisch, J. E. (1974). In *Energy Metabolism of Farm Animals*, European Association for Animal Production Publication no. 14, pp. 131–134 [K. H. Menke, H.-J. Lantzsch and J. R. Reichl, editors]. Hohenheim: Universitat Hohenheim Dokumentationsstelle.

Webster, A. J. F. (1978). *World Review of Nutrition and Dietetics* **30**, 189–226.

Webster, A. J. F., Brockway, J. & Smith, J. S. (1974). *Animal Production* **19**, 127–139.

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