The effect of date of cut and barley substitution on gain and on the efficiency of utilization of grass silage by growing cattle

2. Nutrient supply and energy partition

BY D. E. BEEVER, S. B. CAMMELL, C. THOMAS, M. C. SPOONER, M. J. HAINES AND D. L. GALE

AFRC Institute for Grassland and Animal Production, Animal and Grassland Research Institute, Hurley, Maidenhead, Berkshire SL6 5LR

1. The effect of harvesting date of perennial ryegrass (*Lolium perenne*) on the nutritive value of the resultant silage and the effect of substitution of late-cut silage with barley was examined in growing cattle. The diets comprised early-cut (H) and late-cut (L) silage offered alone or with 280 (LC1) or 560 (LC2) g rolled barley/kg total dry matter (DM) substituted for late-cut silage.

2. Both silages were prepared with the addition of formic acid (850 g/l; 2·4 litres/t fresh weight) to a partially wilted crop, and were judged to be well fermented (pH 3·9, 3·8) with lactic acid contents of 108 and 73 g/kg DM, total nitrogen contents of 24·6 and 18·4 g/kg DM and ammonia-N contents of 121 and 124 g/kg total N (values for early- and late-cut silages respectively).

3. Two experiments were conducted to measure duodenal non-NH$_3$-N (NAN) supply in relation to N intake on the four diets (feeding level 18 g DM/kg live weight (LW)) and to examine the partition of the metabolizable energy (ME) supply from the four diets using open-circuit indirect calorimetry (three feeding levels, 14, 17 and 20 g DM/kg LW). The experiments were undertaken with eight and nine Friesian male castrates respectively with a mean starting weight of 300 kg and age 12 months. The animals used in Expt 1 had been previously fitted with cannulas into the dorsal rumen and the proximal duodenum.

4. NAN supply was significantly higher on diet H than all other diets which were similar irrespective of the level of barley inclusion. Mean ME contents (MJ/kg DM) of the two silages differed markedly (H 11·9, L 9·7) and barley addition (LC1 and LC2) restored values to 10·7 and 11·1 MJ/kg DM respectively. Estimated NAN absorption in relation to energy supply was significantly higher for diet H (1·47 g/MJ ME) than for all other diets (mean 1·25 g/MJ ME).

5. Partition of ME supply using conventional linear analysis indicated dietary differences with respect to estimated ME for maintenance (L > H, LC1 and LC2) and efficiency of utilization of ME supplied above maintenance (L > H, LC1 and LC2), but difficulties in biological interpretation of these findings led to the use of exponential curve analysis. This provided an improved description of the findings, and whilst dietary differences were apparent, none were statistically significant. It was concluded that a single exponential equation could be used satisfactorily to describe all values.

6. The consequence of these findings in relation to the carcass retentions of energy, fat and protein reported by Thomas *et al.* (1988) is discussed and possible reasons for the discrepancies in energy retention measured by comparative slaughter balance and open-circuit indirect calorimetry are considered.

In the previous paper (Thomas *et al.* 1988) the consequence of delaying the harvesting of grass for ensiling on the nutritive value of the resultant silage when offered to beef cattle was examined, and the response to barley substitution of the later-cut material was quantified. That study was concerned with the examination of body and carcass retentions of energy, protein and fat at one feeding level (18 g dry matter (DM)/kg live weight (LW)) using the comparative slaughter technique.

The objective of the present experiment, conducted in parallel with that reported by Thomas *et al.* (1988), was to examine the effect of increasing digestible nutrient intake either through an increase in silage digestibility or through an increase in the proportion of rolled barley given with the low digestibility silage on the supply of protein and metabolizable energy (ME), and the partition and efficiency of utilization of the ingested energy, using conventional digestion and open-circuit calorimetric procedures. The overall

objectives were to provide information which may explain any production responses noted by Thomas *et al.* (1988) and to compare direct (comparative slaughter) and indirect (calorimetry) techniques for the assessment of energy retention. A preliminary report of this study has been published (Beever *et al.* 1984).

MATERIALS AND METHODS
Diets

The diets were as described by Thomas *et al.* (1988), and comprised grass silages made from a pure sward of perennial ryegrass (*Lolium perenne* cv. Melle) harvested on 27 May (early) or 23–27 June (late). Both silages were prepared from partially wilted grass with the addition of formic acid (ADD-F; BP Nutrition International plc; 850 g formic acid/l; 2·4 litres/t fresh weight) and were stored in bunker silos for 5 months before use.

The four diets offered to the animals comprised early-cut silage (H) and late-cut silage alone (L) or substituted with 280 (LC1) or 560 (LC2) g rolled barley DM/kg total DM.

Experimental design

Expt 1 was designed to measure the flow of non-ammonia-nitrogen (NAN) into the small intestine in relation to N intake for the four diets and comprised two 4×4 Latin-Square designs with a total of eight animals. One level of feeding (18 g DM/kg LW) was used. Expt 2 was designed to examine the effect of date of harvest and barley substitution on the ME content of the diets, the efficiency of utilization of ME for growth and fattening, and energy retention using open-circuit indirect calorimetry (Cammell *et al.* 1981, 1986). Each diet was offered at three levels. (14, 17 and 20 g DM/kg LW) to nine steers in four periods (*n* 36, i.e. three observations for each diet at each feeding level). Between periods the animals were re-randomized to diets and feeding levels, such that during the experiment each animal was offered each diet once only, and received each feeding level at least once. Additionally two animals were retained throughout the experiment for the determination of fasting heat production.

Animals and their management

From an initial group of sixty-five British Friesian steers, forty-two and twenty respectively were selected at random for the comparative slaughter balance (Thomas *et al.* 1988), and the present study. From this total, eight animals were selected for Expt 1, and were fitted with PVC cannulas into the dorsal sac of the reticulorumen and the proximal duodenum using previously described techniques (Beever *et al.* 1978), approximately 2 months before the experiment commenced. A further eleven were selected for Expt 2 of which two were subsequently identified for the fasting heat production measurements. The remaining animal was removed from the experiment.

Until commencement of the experiment, all animals were given a medium quality grass hay (*ad lib.*) and barley (restricted), sufficient to sustain a daily LW gain of 0·6 kg. At the start of the experiment, the animals were 12 months old and weighed approximately 300 kg.

The diets were introduced over 14 d and each measurement period within each experiment lasted for approximately 21–28 d after diet change-over. Between periods, all diet change-overs were effected within 7 d. The two animals destined for estimation of fasting heat production were given a mixture (85:15, w/w, DM basis) of early-cut silage and rolled barley (18 g DM/kg LW) until 7 d before the intended period of fast, when feeding level was reduced to 14 g DM/kg LW before fasting. After completion of the measurements, re-alimentation was as described by Cammell *et al.* (1986).

The eight animals for Expt 1 were held in 'resting pens' at all times, and the portable infusion and sampling apparatus developed by Evans *et al.* (1981 *a*, *b*) was used as required. The animals for Expt 2 were housed in 'resting pens' between measurements, and moved, in sequence, to metabolism cages for estimates of faecal and urine output (8 d). Subsequently, they were transferred to similar metabolism cages within the respiration chambers and after 1 d for acclimatization, two 24 h measurements of gaseous exchange were conducted. The cattle were then returned to the 'resting pens' and diet change-overs commenced. Similar procedures were adopted for the fasting animals (excluding measurements of faecal and urine output). No measurements were made on any animal in either experiment until 2 weeks following completion of diet change-over.

All animals were kept in a partially controlled environment with continuous lighting. Fresh water and mineral blocks were freely available, and all animals were fed at 09.00 hours and 16.30 hours each day, when equal amounts of the daily feed allocation were given. Feed refusals, if any, were removed daily at 08.30 hours, weighed and toluene DM determinations were carried out subsequently to estimate actual DM intakes.

Experimental procedure

Expt 1. Intrarumen infusions of ruthenium phenanthroline (RuP) and CrEDTA were commenced 6 d before the collection of duodenal contents. Infusates were adjusted to provide 12 mg ruthenium and 120 mg chromium/kg DM offered, contained in a total volume of 500 ml/d, and were infused continuously into the reticulorumen (20 ml/h) using portable infusion pumps (Evans *et al.* 1981*a*). Subsequently, duodenal digesta collections were undertaken for two 24 h periods using portable samplers (Evans *et al.* 1981*b*), according to the procedures described by Beever *et al.* (1985).

Expt 2. Total faecal and urine outputs were collected concurrently for 8 and 5 d respectively, according to the procedures outlined by Cammell (1977). The animals were subsequently placed in open-circuit calorimeters and the procedures adopted to estimate heat production over two separate 24 h periods were identical to those described by Cammell *et al.* (1986). Measurements of gaseous exchange only were made with the fasted animals.

Preparation and analysis of samples

Samples of the offered feeds, taken at the time of experimental measurements, were frozen and subsequently freeze-dried (silage only) or oven-dried (barley), and ground (as appropriate) through a small laboratory mill. All duodenal-digesta samples were prepared according to Beever *et al.* (1985), to provide samples of whole and centrifuged digesta as outlined by Faichney (1975). These samples were subsequently freeze-dried and ground through a small laboratory mill before analysis.

Individual daily faecal samples for each animal were bulked on a fresh weight basis (Cammell *et al.* 1986) and portions were oven-dried to determine total faecal DM production. Further portions were freeze-dried and ground through a laboratory mill. The daily urine samples were accumulated on a fresh weight basis and subsamples were held frozen for subsequent analysis. A further subsample was dried under reduced pressure (Cammell *et al.* 1986) for determination of urine energy content.

Subsequently, all samples of feed, faeces, urine, duodenal digesta and intrarumen infusates were analysed, as appropriate, for DM (toluene distillation for silages), organic matter (OM), total N, ammonia-N, neutral- and acid-detergent fibre (NDF and ADF respectively), gross energy (GE), and Ru and Cr contents, as described by Thomas *et al.* (1988), Beever *et al.* (1978, 1985), Cammell *et al.* (1986) and Siddons *et al.* (1979).

Calculation of results

Expt 1. Estimates of nutrient flow to the small intestine were obtained using the dual-phase-marker method proposed by Faichney (1975) and related to the quantities of individual nutrients consumed.

Expt 2. Estimates of dietary ME contents and ME intakes (MEI) were derived from estimates of GE intake (GEI), faecal and urine energy output and methane production, using the estimates of CH_4 production derived from the calorimetry experiments appropriately corrected for small differences in DM consumption to those intakes recorded during the corresponding period of faecal and urine collection. Heat production was calculated according to Brouwer (1965) from the observed values for oxygen and carbon dioxide exchange and CH_4 production (all corrected to DM intakes recorded during the balance measurements) and urinary N excretion (as measured). Energy-retention (ER) values were derived as the difference between MEI and heat production.

Two methods of analysis were used to examine the relation between ER and MEI, i.e. linear regression and exponential curve analysis, using both unscaled results and results scaled with respect to metabolic body-weight (kg $LW^{0.75}$). The exponential curve analysis was described by Cammell *et al.* (1986) and used fasting heat production measurements which were obtained from two steers on three separate occasions during the experiment (n 6). These values were included as data points in the analysis, but the curves were not constrained to pass through these data. The equation describing ER in relation to MEI as presented by Cammell *et al.* (1986) was:

$$ER = P_3[1 - \exp(-P_1(MEI - P_2))],$$

where P_1 is the curvature or specific rate of change, P_2 is the maintenance ME, P_3 is the asymptote and $P_3[1 - \exp(P_1 P_2)]$ is the estimation of fasting heat production.

Statistical analysis

Values from Expt 1 were subjected to analysis of variance of a 4×4 Latin-Square design with two animals per sequence. There were four missing values for which estimated values were substituted leaving 14 residual df.

Due to the unbalanced design, values from Expt 2 were analysed using regression analysis by fitting animal, period and diet level effects. A total of six values were not obtained, due mainly to equipment malfunction, in particular aspects associated with data acquisition and retrieval. One of the observations not obtained on diet L was due to the animal's continued inappetance. These six missing values were omitted from the analysis leaving 7 residual df. ER values were analysed using both linear regression and exponential curve fitting.

RESULTS
Chemical composition of the diets

The composition of the two silages and barley are given by Thomas *et al.* (1988). The silages had similar concentrations of DM, GE and ammonia-N (expressed as g/kg total N) and similar pH values whilst total N and total fermentation acids (particularly lactic acid) contents were higher, and fibre and ethanol concentrations lower for the early-cut silage than for the late-cut silage. The barley had a total N content intermediate between those of the two silages, and had a lower fibre content.

Nutrient supply

Values for duodenal flow of NAN, the estimated supply of absorbed NAN/MJ ME and the rumen digestion of NDF are presented in Table 1.

Table 1. *Mean quantities of total nitrogen (or non-ammonia-N (NAN)) and neutral-detergent fibre (NDF) consumed and entering the small intestine of cattle consuming the four grass-silage-based diets, and the estimated supply of NAN per MJ metabolizable energy (ME) consumed*

Diet…	Early-cut silage H	Late-cut silage L	LC1	LC2	SE of means
Total N intake (g/d)	131·0	92·8	102·9	106·8	1·72
NAN flow (g/d)	145·4	104·2	106·3	118·6	3·79
Absorbed NAN* (g/MJ ME)	1·47	1·33	1·17	1·23	0·068
NDF (kg/d):					
Consumed	2·46	3·18	2·64	1·85	0·049
Entering small intestine	0·77	1·44	1·42	1·08	0·064
NDF digestion in rumen (g/kg intake)	687	547	462	416	28·3

H, early-cut silage alone; L, late-cut silage alone; LC1, late-cut silage with 280 g barley dry matter (DM)/kg total DM; LC2, late-cut silage with 560 g barley DM/kg total DM.
  * Assuming small intestinal availability of NAN of 0·63.

N intakes on the three diets based on late-cut silage ranged from 93 to 107 g/d, and a similar range in duodenal NAN flows was obtained, with no evident effect due to barley inclusion. N intake for diet H was approximately 0·30 higher than for the other diets, and this was reflected in an elevated supply of duodenal NAN compared with the other three diets. The average effect of cereal inclusion with the late-cut silage diet was to reduce absorbed NAN supply/MJ ME compared with diet L (1·21 *v.* 1·33 g/MJ), whilst early cutting of grass gave a value of 1·47 g/MJ, if an average small intestinal availability of NAN of 0·63 was assumed for all diets.

NDF intakes were reduced by increased cereal inclusion in the late-cut silage diets, and this was accompanied by a marked reduction in the amount (from 1·74 to 0·77 kg/d) and proportion (from 547 to 416 g/kg) of fibre digested in the rumen. In contrast, for diet H, the proportion of ingested NDF digested in the rumen was 687 g/kg, which was significantly ($P < 0·01$) higher than for all other diets.

Energy metabolism

Values relating to the mean quantities of GE consumed, and lost in the faeces, urine, and CH_4 produced by cattle consuming the four diets at three levels of feeding are given in Table 2. Mean GEI ranged from 96 to 105 MJ/d, and as expected, digestible energy (DE) content per MJ GEI was significantly ($P < 0·05$) higher with diet H (0·742 MJ) than with diet L (0·609) MJ. The values for the two cereal-containing diets were intermediate (0·675 and 0·695 MJ, not significantly ($P > 0·05$) different from each other, but significantly ($P < 0·05$) different from the two silage-only diets. Urine energy was significantly ($P < 0·05$) higher for diet H (0·064 MJ/MJ DE intake (DEI)) than for diets L, LC1 and LC2 (mean 0·044 MJ/MJ DEI); the inclusion of barley appeared to have no effect on urine energy loss. CH_4 energy per MJ GEI was lowest for diet L (0·067 MJ) and increased with barley inclusion to 0·074 (diet LC1) and 0·083 (diet LC2), but only with diet LC2 was the difference statistically significant ($P < 0·05$). The value for diet H (0·073 MJ) was similar to diet LC1 and not significantly different from the other diets. In relation to DEI, CH_4 energy values ranged from 0·098 to 0·118 MJ/MJ, with diet H being significantly ($P < 0·05$) lower than diet LC2.

Table 2. *The mean quantities (MJ/d) of gross energy consumed and energy lost in the faeces, urine and methane produced by animals offered the four grass-silage-based diets*

(Values for the three levels of feeding have been combined*)

Diet...	Early-cut silage H	Late-cut silage			SE of means
		L	LC1	LC2	
No. of replicates...	9	7	8	6	
Gross energy (MJ/d):					
In feed	104·7	96·4	100·0	101·0	2·82
In faeces	27·0	37·7	32·5	30·8	1·36
In urine	4·95	2·79	2·83	3·00	0·709
As methane	7·60	6·44	7·38	8·28	0·485
Apparent digestibility of gross energy	0·742	0·609	0·675	0·695	0·0127
Partition of digestible energy (MJ/MJ)					
Urine	0·064	0·048	0·042	0·043	0·0093
Methane	0·098	0·110	0·109	0·118	0·0060
Metabolizable energy	0·838	0·842	0·848	0·839	0·0134

H, early-cut silage alone; L, late-cut silage alone; LC1, late-cut silage with 280 g barley dry matter (DM)/kg total DM; LC2, late-cut silage with 560 g barley DM/kg total DM.

  * For details, see p. 310.

Table 3. *The mean metabolic body-weights (kg live weight$^{0.75}$) and the intakes of metabolizable energy and the estimates of energy retention when the four grass-silage-based diets were offered at three feeding levels* to growing cattle*

Diet...	Feeding level	Early-cut silage H	Late-cut silage			SE of means
			L	LC1	LC2	
Metabolic body-wt (kg live wt$^{0.75}$)	1	75·54	75·48	75·54	76·61	
	2	74·50	76·27	77·64	76·39	0·693
	3	74·17	78·00	77·74	75·33	
Metabolizable energy intake (MJ/d)	1	55·0	41·3	48·4	50·0	
	2	60·0	52·4	53·4	59·4	2·11
	3	78·5	54·6	68·7	66·7	
Energy retention (MJ/d)	1	8·8	−1·4	6·9	7·7	
	2	12·2	7·9	7·9	11·2	2·32
	3	18·4	7·3	16·7	15·8	

H, early-cut silage alone; L, late-cut silage alone; LC1, late-cut silage with 280 g barley dry matter (DM)/kg total DM; LC2, late-cut silage with 560 g barley DM/kg total DM.

  * For details, see p. 310.

Table 4. *Equations relating energy retention to metabolizable energy (ME) intake (MEI) for cattle consuming the four grass-silage-based diets, and predictions of energy retention based on the curvilinear model*

Diet...		Early-cut silage H	Late-cut silage L	LC1	LC2
Linear regression: unscaled					
Slope (k_f)		0·416	0·588	0·401	0·361
Constant		−13·38	−24·30	−12·28	−9·87
Estimated maintenance					
ME (MJ/d)		32·2	41·3	30·7	27·4
r		0·901	0·778	0·967	0·967
RSD		2·555	2·493	1·713	1·206
Linear regression: scaled					
to metabolic body-wt					
Slope (k_f)		0·433	0·739	0·498	0·433
Constant		−0·193	−0·412	−0·233	−0·189
Estimated maintenance ME					
(kJ/kg $LW^{0.75}$ per d)		445·1	561·0	468·4	455·5
r		0·895	0·799	0·980	0·963
RSD		0·0349	0·0303	0·0153	0·0157
Curvilinear model: unscaled					
P_1 (MJ/MJ)	Mean	0·0140	0·0067	0·0169	0·0219
	SE	0·00506	0·00285	0·00347	0·00240
P_2 (MJ/d)	Mean	37·3	41·6	35·4	33·5
	SE	2·87	0·70	1·65	0·00240
P_3 (MJ/d)	Mean	43·6	93·8	36·6	27·8
	SE	15·60	44·37	7·67	3·05
F_2 (MJ/d)	Mean	29·8	30·0	30·0	30·0
	SE	6·25	6·93	3·67	1·82
Predicted energy retention					
(MJ/d) at MEI (MJ/d) of:					
30		−4·7	−7·5	−3·5	−2·2
40		+1·6	−1·0	+2·7	+3·7
50		+7·1	+5·1	+8·0	+8·4
60		+11·9	ND	+12·4	+12·2
70		+16·0	ND	ND	ND

H, early-cut silage alone; L, late-cut silage alone; LC1, late-cut silage with 280 g barley dry matter (DM)/kg total DM; LC2, late-cut silage with 560 g barley DM/kg total DM; ND, values not determined as MEI outside range of those fed in the experiment; RSD, residual standard deviation; P_1, curvature; P_2, maintenance; P_3, asymptote; F_2, fasting heat production; k_f, predicted efficiency of utilization of ME; LW, live weight.

Dietary ME contents ranged from 9·73 MJ/kg DM (diet L) to 10·66 and 11·07 MJ/kg DM (diets LC1 and LC2) in response to barley inclusion, compared with a value of 11·93 MJ/kg DM for diet H. For all diets, ME averaged 0·842 of DE, whilst metabolizability (ME:GE) of the diets increased from 0·52 (L) to 0·58 and 0·59 (diets LC1 and LC2) compared with 0·62 (diet H).

In Table 3, metabolic body-weight, MEI and estimated ER for all diets at each feeding level are presented. Linear regressions (both unscaled and scaled to metabolic body-weight) and exponential curve analysis (unscaled only) of ER *v.* MEI are presented in Table 4.

With diets LC1, LC2 and H, the range in daily MEI (level 1–level 3) varied between 17

and 24 MJ. Unfortunately, due to some feed refusals, the range was lower on diet L (13 MJ), reflecting the difficulty in achieving consistent intakes in excess of 17–18 g DM/kg LW on this diet. Across all diets, daily MEI ranged from 41 to 79 MJ/d with ER of -1.4 to $+18.4$ MJ/d.

Using unscaled values, predicted values for efficiency of utilization of ME(k_f) for the two cereal-containing diets and diet H were not significantly different ($P > 0.05$; mean 0.39) but were markedly lower than the value for diet L. Estimated ME requirements for maintenance (P_2) were 27.4 to 32.2 MJ/d for diets LC1, LC2 and H, compared with 41.3 MJ/d for diet L. Scaling the values to metabolic body-weight did not markedly change the situation. k_f for diets H, LC1 and LC2 increased by 2–9 percentage units with a mean P_2 requirement of 456 kJ/kg LW$^{0.75}$ per d. These values contrasted with unrealistically high values of k_f (0.74) and P_2 cost (561 kJ/kg LW$^{0.75}$ per d) for diet L.

With exponential curve analysis, P_2 estimates ranged from 33.5 to 41.6 MJ/d, suggesting higher values for the two forage diets (39.5 MJ/d) than for the cereal-containing diets (34.5 MJ/d). All predicted fasting heat production values (mean 30.0 MJ/d) were close to the measured values (mean 29.9 MJ/d). As MEI increased on all diets the relations suggested that positive ER would occur first on diet LC2, followed by diets LC1, H and L, in that order. However, the rate of decline in ER with increasing MEI was estimated to be greatest on diet LC2 (0.022 MJ/MJ) followed by diets LC1 and H (mean 0.016 MJ/MJ), and all markedly higher than the value obtained on diet L (0.007 MJ/MJ). Using these equations to predict ER at variable MEI within the range of MEI observed in the experiment, it can be seen that at MEI between 40 and 50 MJ/d ER tended to be higher on the two cereal-containing diets whilst at intakes of 60 MJ ME/d, all diets (except diet L) gave predicted ER of approximately 12 MJ/d. With diet L, on the basis of the intakes achieved in the present experiment, it would appear that ER in excess of 5 MJ/d (predicted) to 7 MJ/d (observed) are unlikely to be achieved in practice.

Exponential curve analysis of the values scaled to metabolic body-weight did not significantly alter the relations, and this analysis is not presented.

Further examination of the unscaled values for energy partition was undertaken by (1) combining the values according to feed type (i.e. silage only and cereal-containing diets) and (2) by combining all values using both the linear and exponential models. From an examination of the resultant analysis it was established that, as compared with an analysis of all values, separate equations for the two feed types did not account for a significantly greater proportion of the variation. Consequently, one overall relation, based on exponential curve analysis is presented as the most appropriate one to describe the values. The terms derived from this analysis are:

P_1 0.0140 (SE 0.00267), P_2 37.57 (SE 1.132), P_3 43.25 (SE 8.049), F_2 29.93 (SE 3.316),

indicating a mean P_2 requirement of 37.6 MJ/d and a predicted fasting heat production (F_2) of 29.93 MJ/d, giving an 'overall' K_m between fasting and maintenance of 0.796.

DISCUSSION

Previous studies which have examined the digestion of non-additive or formic-acid-treated grass silages (Beever *et al.* 1971, 1977; Møller & Thomson, 1977; Kelly *et al.* 1978; Siddons *et al.* 1979; Beever, 1980) have consistently demonstrated reduced duodenal NAN flows with respect to N intake, whilst Thomson & Beever (1980) showed small-intestinal uptake of amino acid-N from wilted and direct-cut silage to be only 0.31 and 0.41 respectively of N intake. In contrast, duodenal NAN supplies in the present study were 1.12 and 1.11 of total N intake for the late- and early-cut silages. The late-cut silage had a low N content

(19·6/kg OM) and, on the basis of relations which have been established between duodenal NAN flow (in relation to N intake) and N content in the dietary OM (Hogan & Weston, 1970; Beever *et al.* 1986*a*; Ulyatt *et al.* 1988), albeit predominantly for fresh forages, a net gain in duodenal NAN flow in relation to N intake could be expected. Conversely, the early-cut silage contained 26·7 g N/kg OM, which would suggest a reduced duodenal NAN flow compared with N intake. The results obtained did not, however, support this suggestion and the elevated duodenal NAN supply was unexpected. Recently, Beever *et al.* (1986*b*) reported similar rumen gains of N when formic-acid-treated grass silage was given with a low-protein concentrate to dairy cows.

Barley substitution of the late-cut silage had only a marginal effect on duodenal NAN supply, such that all diets based on late-cut silage gave an estimated NAN absorption of between 1·17 and 1·33 g/MJ ME compared with 1·47 g/MJ ME for the early-cut silage. The possibility of an increased passage of starch to the small intestine of cattle on the barley diets was not examined, but the consequence of increased cereal consumption on fibre digestion in the rumen was detected. Although NDF consumption was highest on diet L, the amount degraded in the rumen was identical (1·72 kg/d) for the two silage-only diets, and hence the proportion of ingested NDF digested in the rumen was lower on diet L. The extent and proportional digestion of ingested NDF declined further, as the level of cereal substitution was increased, in line with the changes in NDF digestibility reported by Thomas *et al.* (1988).

The production experiment reported by Thomas *et al.* (1988) clearly identified dietary differences with respect to ER, and from a comparison of diets H and LC2 it was concluded that in order to achieve similar levels of ER on both diets, it would be necessary to increase ME supply on early-cut silage by approximately 9%.

ER determined by calorimetry were found on all diets at the highest level of feeding to be higher than those estimated by comparative slaughter, with the positive effect of cereal inclusion being most evident. This was apparent even when differences in intake between the two experiments were taken into account. Contrary to the findings obtained from the slaughter experiment, the ER derived by calorimetry for diet H exceeded those obtained for diet LC2. However, linear regression analysis of the values for the individual diets failed to establish significant differences between diets H, LC1 and LC2 with respect to k_f and estimates of P_2 costs. In contrast, a major problem with respect to diet L was identified. Both the patterns of feed intake and measurement of heat production were quite erratic on this diet, especially when the highest level of feeding was being offered. Thus the range in MEI in the experiment was reduced and this, combined with increased variations in daily heat production (and hence ER), led to linear analysis of the values for diet L giving relatively imprecise relations and biologically irreconcilable results. Use of exponential curve analysis was unlikely to improve this situation for diet L, and when the values for the two forages were combined, the effects of the late-cut silage values were still evident. Thus whilst the ER values presented in Table 3 indicated the inferiority of diet L, it was not statistically possible to describe the values other than by a single exponential curve for all diets.

This problem of low ER with low-quality diets of low intake potential has been encountered in other studies (Thomson *et al.* 1979). With hindsight it may have been advisable to extend the period of measurement for gaseous exchange with animals receiving the late-cut silage. In the present experiment only 2 d of measurement were made, but it would have been feasible to increase this to at least 4 d, which should have provided an improved data-base relating feed intake to heat production. Second, it may have been advisable to increase the number of observations on this diet.

Using the overall exponential relation derived for all diets it was possible to predict ER

Table 5. *Comparison of energy retentions (MJ/d) estimated by comparative slaughter (CST), predicted from the overall exponential relation derived from the calorimetric studies (CAL) and predicted from Agricultural Research Council (1980) using separate (ARC-S) or an overall (ARC-O) relation*

Diets...	Early-cut silage H	Late-cut silage			MSPE (MJ²)	Bias (MJ)	SE of means
		L	LC1	LC2			
CST	12·24	5·48	9·23	14·58	—	—	—
CAL	17·07	11·15	13·88	15·16	22·62	4·04	1·80
ARC-S	18·04	9·50	13·27	15·65	19·97	3·73	1·77
ARC-O	18·41	8·66	14·55	16·83	23·48	4·23	1·70

H, early-cut silage alone; L, late-cut silage alone; LC1, late-cut silage with 280 g barley dry matter (DM)/kg total DM; LC2, late-cut silage with 560 g barley DM/kg total DM; MSPE, mean square prediction error (for details, see Bibby & Tentenburg (1977) and Theil (1966)).

ARC-S: Forage diets $k_f = 1.32 q_m - 0.318$,
Mixed diets $k_f = 0.38 q_m + 0.282$,
ARC-O: All diets $k_f = 0.78 q_m + 0.006$,

where k_f is the predicted efficiency of utilization of metabolizable energy for growth and fattening and q_m is the measured metabolizability of the gross energy of the diet.

in the animals used in the comparative slaughter balance (Thomas *et al.* 1988) using actual DM intakes recorded in that experiment and the ME concentrations derived in the present study. The values are presented in Table 5 along with predicted ER using relations proposed by the Agricultural Research Council (1980) for all diets (ARC-O) or for forage and mixed diets separately (ARC-S).

For all diets, except L, there was a reasonably close agreement between the predicted ER, values based on calorimetry and those predicted by the calorimetrically-based Agricultural Research Council (1980) system (ARC-S, ARC-O), whilst the calorimetry-derived value for diet L was approximately 2 MJ/d higher than that predicted on the basis of ARC-O and ARC-S. However, only with diet LC2 was there an acceptable agreement between the prediction of ER derived by calorimetry and that estimated by comparative slaughter. With the other diets it was clear that there was a considerable over-prediction amounting to between 3 and 6 MJ/d, equivalent to an increased daily LW gain of 0·25 kg based on the energy value of gain determined by Thomas *et al.* (1988). This apparent discrepancy between ER estimates based on comparative slaughter and calorimetry in the present study using similar diets fed to virtually identical cattle, has been illustrated by others (Bull *et al.* 1976) but it remains difficult to establish the major causes of the effect. Failure in the present study to establish specific dietary relations between energy intake and ER and the consequential use of a combined relation may have contributed to this discrepancy. It is interesting to note from the comparison presented in Table 5 that the largest discrepancies were detected on diets L and LC1 which were the diets which promoted the lowest energy gains. Environmental conditions prevailing at the time of experimentation may in part have contributed to the effect. The animals used in the comparative slaughter balance were maintained at ambient temperature (approximately $-3°$ to $+6°$) compared with the higher temperatures (14°) to which the animals used for calorimetry were subjected. Additionally, activity costs would have been greater with the animals in the comparative slaughter study.

However, even together, these aspects seem unlikely to account for a major part of the differences observed in ER. An additional consideration is that the heat production measurements were obtained indirectly from measurement of gaseous exchanges and it may be that the equation proposed by Brouwer (1965) to calculate heat production from gaseous exchange is not applicable to all dietary circumstances. With respect to acclimatization of the animals before measurements of gaseous exchange, the trend towards a reduced heat production was opposite to that which would be expected if the animals responded adversely to their new environment, and consequently problems in acclimatization can be ruled out as a source of error.

In a recent review of methodological problems associated with ER studies, Graham (1982) referred to the general overprediction of ER and hence underprediction of energy requirement which occurs with the Agricultural Research Council (1980) system, which was derived from calorimetric values, is compared with the National Research Council (1970) system which is based on slaughter balance, and cited the studies of Graham & Searle (1972) where, for the same diets offered to sheep, k_f estimates based on calorimetry were 0·50–0·60 compared with values of 0·30–0·40 derived from slaughter experiments. In attempting to resolve this discrepancy, Graham (1982) suggested that there is an appreciable energy expenditure associated with the physiological state of immature animals and that this state responds rather slowly to changes in feed intake. Thus Graham (1982) concluded that in short-term calorimetry studies, where animals are changed from one diet to another, there is generally insufficient time for the animals to adapt fully to their new nutritional state and such experimental procedures may limit the general applicability of the values obtained by calorimetry. This issue is also discussed by Turner & Tayler (1983) and is now being investigated experimentally in this laboratory, in order that some of the discrepancies between comparative slaughter and calorimetry may be resolved.

It would, however, be premature to suggest that all the errors lie within the calorimetric estimates of ER. In this respect Thomas *et al.* (1988) high-lighted possible inaccuracies as a result of errors in the estimation of fat content of gain arising from a relatively poor relation between weight of fat and empty-body-weight in the initial slaughter group, and the method of fat analysis used. If the average error of underestimation of 8–9 % in fat content derived by Woodward *et al.* (1976) using the Foss-let method, as used by Thomas *et al.* (1988), is applied to the values in Table 5, then ER estimated by comparative slaughter would increase and the change would account for between 7 and 20 % of the difference between calorimetric and comparative slaughter estimates. Nevertheless a considerable between-method difference would continue to exist and reconciliation of such remains a research priority.

When the intakes of ME and the levels of absorbed NAN were computed for the animals used in the production study (Thomas *et al.* 1988) and related to empty-body retentions of energy, protein and fat (see Table 6), some interesting differences in the utilization of ME and absorbed NAN were observed. Thus whilst total ME, absorbed NAN and absorbed NAN/MJ ME were all higher for diet H than for diet LC2, the highest empty-body retentions of energy, protein and fat were recorded on the high-cereal diet. Even when the values were expressed in relation to ME available for production, using the P_2 requirements given in Table 4, the performance differences still existed. On the basis of current systems designed to meet the energy and protein requirements of growing ruminants (Agricultural Research council, 1980, 1984), it would not be possible to predict such variations in animal response. This indicates a weakness in the present systems in that the factors governing the partition of absorbed nutrients are not sufficiently well represented. It must be concluded that explanation for such responses lies at a more fundamental biochemical level than

Table 6. *The effect of stage of harvest and barley supplementation on energy and protein supply and the retention of energy, protein and fat in growing cattle*

| | Early-cut silage | Late-cut silage | | |
Diet...	H	L	LC1	LC2
ME intake (MJ/LW$^{0.75}$ per d)	0·93	0·76	0·83	0·87
NAN supply (g/LW$^{0.75}$ per d)	2·14	1·60	1·54	1·72
Absorbed NAN/ME supply (g/MJ)	1·47	1·33	1·17	1·23
Empty body				
Energy retention (MJ/d)	12·2	5·5	9·2	14·6
Protein (g/d)	87	31	76	116
Fat (g/d)	260	121	189	302

H, early-cut silage alone; L late-cut silage alone; LC1, late-cut silage with 280 g barley dry matter (DM)/kg total DM; LC2, late-cut silage with 560 g barley DM/kg total DM; ME, metabolizable energy; NAN, non-ammonia-nitrogen; LW, live weight.

simply the provision of ME and absorbed protein, and that the importance of the nature of ME with respect to individual nutrients must be recognized. It is pertinent to note that Thomas *et al.* (1988) demonstrated that the proportion of the ME derived from digestible cell walls varied markedly with diet type and concluded that the level of animal performance achieved appeared to be inversely related to the contribution from cell-wall materials. Clearly, this suggests that a fuller description of the nature of the ME will be required if animal responses are to be predicted accurately from a knowledge of the diet consumed. Only once the precise causes of the animal responses noted in the present and other similar studies are fully understood will the full impact of the effect of harvesting date of grass, and the strategic use of supplements, on ruminant livestock systems be realizable in practice.

REFERENCES

Agricultural Research Council (1980). *The Nutrient Requirements of Farm Livestock* no. 2, *Ruminants*. Farnham Royal: Commonwealth Agricultural Bureaux.
Agricultural Research Council (1984). *The Nutrient Requirements of Farm Livestock* no. 2, *Ruminants*, Suppl. no. 1. Farnham Royal: Commonwealth Agricultural Bureaux.
Beever, D. E. (1980). In *Forage Conservation in the 80's, Proceedings of European Grassland Federation Meeting, Brighton. British Grassland Society Occasional Publication* no. 11, pp. 131–143 [C. Thomas, editor]. Hurley, Maidenhead, British Grassland Society.
Beever, D. E., Cammell, S. B., Haines, M. J., Gale, D. L. & Thomas, C. (1984). *Animal Production* **37**, 533.
Beever, D. E., Dhanoa, M. S., Losada, H. R., Evans, R. T., Cammell, S. B. & France, J. (1986a). *British Journal of Nutrition* **56**, 439–454.
Beever, D. E., Kellaway, R. C., Thomas, D. J., MacRae, J. C., Evans, C. C. & Wallace, A. S. (1978). *Journal of Agricultural Science, Cambridge* **90**, 157–163.
Beever, D. E., Thomson, D. J., Cammell, S. B. & Harrison, D. G. (1977). *Journal of Agricultural Science, Cambridge* **88**, 61–70.
Beever, D. E., Thomson, D. J., Pfeffer, E. & Armstrong, D. G. (1971). *British Journal of Nutrition* **26**, 123–134.
Beever, D. E., Thomson, D. J., Siddons, R. C. & Thomas, C. (1986b). *Journal of Dairy Science* **69**, 219.

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.

Bibby, J. & Tentenburg, H. (1977). *Prediction and Improved Estimation in Linear Models*. London: John Wiley & Sons.

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

Bull, L. S., Tyrrell, H. F. & Reid, J. T. (1976). *Energy Metabolism of Farm Animals, European Association of Animal Production Publication* no. 19, p. 137–140.

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

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

Cammell, S. B., Thomson, D. J., Beever, D. E., Haines, M. J., Dhanoa, M. S. & Spooner, M. C. (1986). *British Journal of Nutrition* **55**, 669–680.

Evans, R. T., Hayes, D. G. & Beever, D. E. (1981 a). *Laboratory Practice* **30**, 591–593.

Evans, R. T., Skelton, K. V. & Beever, D. E. (1981 b). *Laboratory Practice* **30**, 997–1000.

Faichney, G. J. (1975). In *Digestion and Metabolism in the Ruminant*, pp. 277–291 [I. W. McDonald and A. C. I. Warner, editors]. Armidale, Australia: University of New England Publishing Unit.

Graham, N. McC. (1982). *Energy Metabolism of Farm Animals, European Association of Animal Production Publication* no. 29, pp. 108–111.

Graham, N. McC. & Searle, T. W. (1972). *Australian Journal of Agricultural Research* **23**, 97.

Hogan, J. P. & Weston, R. H. (1970). In *Physiology of Digestion and Metabolism in the Ruminant*, pp. 474–485 [A. T. Phillipson, editor]. Newcastle upon Tyne: Oriel Press.

Kelly, N. C., Thomas, P. C. & Chamberlain, D. G. (1978). *Proceedings of the Nutrition Society* **37**, 34A.

Møller, P. D. & Thomson, K. V. (1977). *Institut for Husdjurens Utfordring och vard, Rapport* no. 54, pp. 27–54.

National Research Council (1970). *Nutrient Requirements of Beef Cattle*, 5th ed. Washington DC: National Academy of Sciences.

Siddons, R. C., Evans, R. T. & Beever, D. E. (1979). *British Journal of Nutrition* **42**, 535–545.

Theil, H. (1966). *Applied Economic Forecasting*, Chapter 2. Amsterdam: North Holland Publishing Company.

Thomas, C., Gibbs, B. G., Beever, D. E. & Thurnham, B. R. (1988). *British Journal of Nutrition* **60**, 297–306.

Thomson, D. J. & Beever, D. E. (1980). In *Digestive Physiology and Metabolism in Ruminants*, pp. 291–308. [Y. Ruckebusch and P. Thivend, editors.] Lancaster: MTP Press Ltd.

Thomson, D. J., Fenton, J. S. & Cammell, S. B. (1979). *British Journal of Nutrition* **41**, 223–229.

Turner, H. G. & Tayler C. S. (1983). *World Review of Nutrition and Dietetics* **42**, 135–190.

Ulyatt, M. J., Thomson, D. J., Beever, D. E., Evans, R. T. & Haines, M. J. (1988). *British Journal of Nutrition* **60**, 137–149.

Woodward, C. J. H., Trayhurn, P. & James, W. P. T. (1976). *British Journal of Nutrition* **36**, 567–570.

Printed in Great Britain