Fat and protein metabolism in growing steers fed either grass silage or dried grass

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Cattle fed grass silage have been reported to have high carcass fat:protein ratios. The effect of grass silage and dried grass diets, fed at different levels of intake to ensure a range of equivalent metabolisable energy intakes (MEI) from 1·1 × metabolisable energy requirement for maintenance to ad libitum, on fat and protein metabolism in twenty-four Hereford × Friesian steers was investigated. After about 84 d of dietary treatment rates of whole-body fat and protein metabolism were measured, as were rates of lipogenesis in omental, perirenal and subcutaneous adipose tissue. Carcass composition was determined. Animals fed silage had greater (P<0·001) carcass fat:protein ratios than animals fed dried grass at equivalent levels of MEI. Animals fed silage had lower (P<0·001) rates of protein gain. Rates of leucine entry and oxidation were lower (P<0·001) in animals fed silage, but there was no dietary difference in the rate of whole-body protein synthesis. There was no dietary difference in the rate of carcass fat gain, but rates of lipogenesis in perirenal adipose tissue were significantly (P=0·007) higher in animals fed silage. There was no dietary difference in the rate of palmitate and glycerol entry or palmitate oxidation. There were no interactions between MEI and diet, indicating that increments of energy were utilised with the same efficiency from both diets. It was concluded that the high carcass fat:protein ratios of young growing steers was due to limited rates of protein accretion and not to elevated rates of carcass fat accretion.

Ruminants: Grass silage: Dried grass: Fat metabolism: Protein metabolism: Carcass composition: Metabolisable energy

Grass silage forms the basis of many winter diets fed to beef cattle in the UK. The performance of animals fed silage is variable and often disappointing in terms of feed intake and the overall efficiency of energy (Thomas & Chamberlain, 1990) and amino acid (Beever et al. 1992; MacRae et al. 1995) utilisation. It has been reported that animals fed silage have a high carcass fat:protein ratio (Lonsdale, 1976; Moore & Steen, 1983; Baker et al. 1985, 1992; Steen & Moore, 1988, 1989; Steen, 1991). That protein deposition is limited in animals fed grass silage is now well established (Gill et al. 1987). Whether or not fat deposition is increased in these animals is unclear.

With continuing pressures to increase the utilisation of grass in ruminant production systems, a greater understanding of the partition of nutrients between fat and protein deposition in animals fed grass silage is required if useful models to predict animal performance are to be developed. The objective of the present study was to determine whether or not an increased fat deposition contributes to the high carcass fat:protein ratio of animals fed grass silage by simultaneously investigating fat and protein metabolism, using isotope dilution and incorporation techniques, and carcass composition of young, growing steers fed either grass silage or dried grass. As both the quantity and form of metabolisable energy (ME) are considered to be important determinants of animal performance (Beever et al. 1988; Thomas & Gill, 1988; Steen, 1992; Steen & Robson, 1995), the animals were fed silage or dried grass at different levels of intake to ensure a range of equivalent ME intakes (MEI), based on the animals’ estimated ME requirement for maintenance (MEm), with the objective of determining whether or not metabolism and carcass composition respond differentially to MEI from the two diets.

Materials and methods

Animals and experimental design

Thirty Hereford × Friesian steers were used, from which twenty-four were randomly selected and assigned a treatment in a 2 (diet: silage and dried grass) × 5 (MEI: 1·1, 1·2, 1·3, 1·4 and 1·5 × MEm) factorial experiment with two additional levels of dried grass MEI (1·8 and 2·0 × MEm), such that there were two steers per diet per MEI level. Animals were paired ensuring a minimal weight range between paired animals, and a similar weight range across dietary treatments. The six remaining steers were slaughtered at the start of

Abbreviations: IGF-I, insulin-like growth factor 1; KKCF, kidney knob and channel fats; LW, live weight; MADF, modified acid detergent fibre; ME, metabolisable energy; MEI, ME intake; MEm, ME requirement for maintenance; Ra, rate of appearance.

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the experiment for carcass composition analysis (initial slaughter group).

The animals fed silage at 1.5 × MEm and dried grass at 2.0 × MEm were actually fed to appetite (fed 10% in excess of the previous day’s refusals), with these intake levels representing the average ad libitum intakes of the animal in each pair with the highest intake over the experimental period. Animals fed dried grass at 1.5 × MEm were restricted to the voluntary MEI level of their silage-fed pair.

From weaning until the start of the experiment (approximately 5 weeks), the steers were group-penned on straw and fed Calf Starter (BOCM Pauls plc, Ipswich, Suffolk, UK) and hay. During this period the average live weight (LW) gain of the animals was 0.42 (SD 0.11) kg/d. At the start of the experiment the steers were approximately 13 weeks of age (mean LW: 94.2 (SD 7.2) kg). The steers were panned individually on rubber matting. The experimental period lasted approximately 13 weeks with all cattle spending the final 2 weeks in metabolism crates. During the whole duration of the experiment, except when animals were in the metabolism crates, steers were weighed twice weekly and their dietary intakes adjusted accordingly. They were fed equal-sized meals twice daily, and had free access to water and mineral licks (Standard Wright Blocks; Frank Wright Ltd, Ashbourne, Derbyshire, UK) at all times.

Once in metabolism crates steers were not weighed. Dietary feeding levels were adjusted according to previous rates of LW gain using linear regression. Final LW was determined in the same way. Diets were fed hourly using automatic feeders. The steers were allowed a 7 d adjustment period to the diets. Diets were fed hourly using automatic feeders. The steers were allowed a 7 d adjustment period to the experimental diets. Feed intake levels were determined based on the steers’ estimated MEm, which were calculated using the equation:

$$\text{ME}_m (\text{MJ/d}) = \frac{(LW \times 0.061) + 5.67}{k_m},$$

where $k_m$ is the efficiency with which ME is used for maintenance and was assumed to be 0.72 (Agriculture and Food Research Council, 1993). The intakes of DM, ME and total N used in this analysis are the average intakes recorded over the period prior to entering metabolism crates.

**Preparation of infusates**

[1-13C]Leucine. The [1-13C]leucine (99.3 atom% 13C; MassTrace Inc., Woburn, MA, USA) was infused (3.3 μg [1-13C]leucine/kg LW per ml infused at 2 μl/min) and priming dose (393 μg/kg LW) were prepared as described by Dawson et al. (1998). The [1-13C]palmitate and [2-3H]glycerol. The [1-13C]palmitate (99 atom% 13C; MassTrace Inc.) was infused (2.5 μg [1-13C]palmitate/kg LW per ml infused at 2 μl/min) was prepared as described by Dawson et al. (1998). To this was added [2-3H]glycerol (355 GBq/mmol; ICN Biomedicals Ltd, Thame, Oxfordshire, UK) such that the final specific radioactivity of the infusion was 0.23 kBq/kg LW per ml.

$\text{NaH}^13\text{CO}_3$ and [1-14C]acetate. The $\text{NaH}^13\text{CO}_3$ infusion (8.0 μg NaH$^13\text{CO}_3$ (kg LW)$^{0.75}$ per ml infused at 2 μl/min) was prepared in saline bags (0.9% (w/v) NaCl; Baxter Healthcare Ltd, Thetford, Norfolk, UK). NaH$^13\text{CO}_3$ (99 atom% 13C; MassTrace Inc.) was dissolved in a small volume of saline from the saline bag and the resulting solution sterilised (0.2 μm Minisart syringe filter; Sartorius GmbH, Göttingen, Germany) as it was returned back to the saline bag. To this was added [1-14C]acetate (2.2 GBq/mmol; ICN Pharmaceuticals Ltd, Thame, Oxfordshire, UK) such that the final specific radioactivity of [1-13C]acetate was 0.5 kBq/kg LW per ml.

Priming doses of NaH$^13\text{CO}_3$ were administered immediately before the start of the [1-13C]leucine, the combined [1-13C]palmitate/[2-3H]glycerol (106.3 μg NaH$^13\text{CO}_3$/kg LW) and the combined NaH$^13\text{CO}_3$/[1-14C]acetate (136 μg NaH$^13\text{CO}_3$ (kg LW)$^{0.75}$) infusions. Priming doses were prepared in 20 ml saline and then filter-sterilised (0.2 μm Minisart syringe filter).

Priming doses of NaH$^13\text{CO}_3$ and [1-13C]leucine were administered to ensure that stable equilibrium [13C]-enrichments were rapidly achieved for expired CO$_2$ and plasma leucine, respectively, due to the slower fractional turnover rates of the plasma NaHCO$_3$ (Allsop et al. 1978) and leucine (Matthews et al. 1980) pools.

**Experimental procedures**

On the fourth day that steers were in metabolism crates, both of their jugular veins were fitted with indwelling cannulae and
kept patent by daily flushing with 3·8 % (w/v) tri–sodium citrate in sterile saline (0·9 % NaCl).

On the eighth day in metabolism crates the steers received a NaH¹³CO₃, and [¹-¹³C]leucine–primed 6 h continuous intravenous infusion of [¹-¹³C]leucine to determine the rate of appearance (Ra) of plasma leucine and the rate of leucine oxidation.

On the ninth day in metabolism crates each steer received a NaH¹³CO₃–primed 6 h continuous intravenous infusion of [¹-¹³C]palmitate and [²-¹³H]glycerol, for determination of the Ra of plasma palmitate and the rate of palmitate oxidation, and determination of the Ra of plasma glycerol, respectively. A 1 d ‘rest period’ followed to allow clearance of residual ¹³C label remaining from the previous infusions.

On the eleventh day in metabolism crates each steer received a combined, NaH¹³CO₃–primed, 6 h continuous intravenous infusion of NaH¹³CO₃ and [¹-¹³C]acetate, for determination of the Ra of whole-body CO₂ and rates of acetate incorporation into lipid, respectively. At the end of the 6 h infusion the steers were killed with a lethal dose of pentobarbitone (Euthates®, 200 g pentobarbitone sodium/l; Williams Francis Veterinary, Crawley, West Sussex, UK) and exsanguinated. Adipose tissue samples from the subcutaneous (tailhead region), omental and perirenal depots were taken within 2 min of death. The carcass was then dressed, weighed and halved. Samples of blood and breath were taken at 30 min intervals for a period of 2 h before the start of the infusions, for the determination of background levels of isotope. Following the start of the infusions breath samples were taken at 15 min intervals for the first 2 h, and then at 30 min intervals until the end of the infusions; blood samples were taken at 30 min intervals throughout the infusions. Blood samples taken on the day of the combined [¹-¹³C]palmitate/ [²-¹³H]glycerol infusion were collected into tubes containing K-EDTA (15 µg/ml blood). All other blood samples were collected into tubes containing heparin (25 units/ml blood). Plasma was isolated from the blood samples by centrifuging at 1000 g for 15 min, which was then stored in a freezer (approximately –20°C) until analysed.

Breath samples were collected into 2-litre breath bags, fitted with one-way valves, via a facemask that was placed over the animal’s nostrils. Triplicate samples of breath were drawn from the bag into evacuated tubes and stored at room temperature until analysed.

Adipose tissue samples were prepared as described by Greathead et al. (2001). From both halves of the dressed carcass, the kidney knob and channel fats (KKCF) were dissected, pooled and weighed. The longissimus dorsi and semitendinosus muscles were dissected from the left half of the carcass and weighed. The entire right half of the carcass (excluding the kidney and KKCF) was weighed and then frozen (approximately –20°C) for subsequent compositional analysis.

Analytical methods

Dietary analysis. The chemical composition of the silage and dried grass were determined as described by Scollan et al. (2001).

Plasma palmitate ¹³C-enrichment and concentration. These were determined by a modified version of the method described by Hachey et al. (1991). The modification involved substitution of the derivatising agent pentafluorobenzyl bromide with iodomethane such that fatty acid methyl esters rather than pentafluorobenzyl esters were formed, enabling analysis by electron impact-GCMS.

Plasma NEFA concentration. These were determined colorimetrically using a commercially available assay kit (NEFA-C, Wako 994-75 409; Alpha Laboratories, Eastleigh, Hampshire, UK).

Plasma leucine and ketoisocaproic acid ¹³C-enrichment and concentration. Using the method described by Calder & Smith (1988), amino acids and keto acids were first isolated from plasma, then transformed to t-butyldimethylsilyl and quinoxalinol-t-butyldimethylsilyl derivatives respectively, and finally analysed by electron impact-GCMS.

Breath ¹³CO₂-enrichment. The ¹³C-enrichment of expired air was determined with a Europa Scientific Tracermass IRMS (Europa Scientific, Crewe, Cheshire, UK). Breath samples were introduced to the isotope ratio mass spectrometer using Roboprep-G (Europa Scientific). Samples were measured against a standard reference gas of 5 % CO₂ in air of known ¹³C-enrichment.

Specific radioactivity of plasma glycerol. Plasma samples were deproteinised with perchloric acid (6 %, v/v) according to the method of Somogyi (1945). The concentration of glycerol in the deproteinised plasma was measured spectrophotometrically using a commercial glycerol assay kit (catalogue no. 148270; Boehringer Mannheim GmbH, Mannheim, Germany). The specific radioactivity of deproteinised plasma glycerol was determined using a modified version of the method described by Symonds et al. (1989), which involved using Dowex 1 (OH⁻ form, 200–400 mesh) ion-exchange resin to trap glucose in place of Dowex 1 (borate form, 200–400 mesh).

Specific radioactivity of plasma acetate, and total lipid extraction and specific radioactivity determination from adipose tissue

These were determined using methods described by Greathead et al. (2001).

Plasma insulin concentration. Plasma insulin concentrations were measured using a commercially available RIA kit (INS-RIA-100; Lifescreen Ltd, Watford, Hertfordshire, UK). Chemical compositional analysis of carcass and muscle samples. This was determined using methods described by Gibb & Baker (1992).

Calculations

Initial carcass composition and live weight gains. Gains in carcass weight and its chemical components were calculated as the difference between the measured component at slaughter and the initial value estimated from regression analysis (Table 1) on the values derived from the initial slaughter group. The mean LW of the initial slaughter group at slaughter was 94·7 (SD 10·10) kg. The average LW gains of the steers were determined by linear regression using the twice-weekly measured LW of the steers.

Rates of appearance, oxidation, whole-body protein synthesis and acetate incorporation into lipid. In all cases,
stable equilibrium $^{13}$C- and $^{14}$C-enrichments were achieved within 2 h of the start of the continuous infusions. The rates of appearance of palmitate and total-body CO$_2$ were calculated by dividing the infusion rate of the tracers [1-1$^{13}$C]palmitate and NaH$^{13}$CO$_3$ respectively, by the tracer:tracee ratios of palmitate and NaHCO$_3$ (measured as breath CO$_2$) respectively, at isotopic equilibrium. Tracer:tracee ratios were determined as described by Dawson et al. (1999).

The rate of plasma leucine appearance was calculated using the equation described by Wolfe et al. (1980). The plasma $^{13}$C-enrichment of ketoisocaproic acid rather than leucine was used in the equation on the assumption that it more accurately reflects the true intracellular precursor pool enrichment (Matthews et al. 1982).

Rates of plasma glycerol and acetate appearance were calculated by dividing the infusion rate of the labelled substrate, [1-1$^{14}$C]glycerol and [1-1$^{14}$C]acetate respectively, by the specific radioactivity of the substrate at isotopic equilibrium (Pethick & Dunshoe, 1993).

The oxidation rates of palmitate and leucine were calculated using the equation:

\[
\text{Oxidation rate (\mu mol/min per kg$^{0.75}$)} = \frac{\Delta \text{P} \text{AP} \text{E}_{\text{CO}_2} \times \text{Rac}_{\text{CO}_2}}{\text{APE}_{\text{S}}},
\]

where $\Delta \text{P} \text{AP} \text{E}_{\text{CO}_2}$ is the isotopic enrichment of expired CO$_2$ at isotopic equilibrium measured during the continuous infusion of [1-1$^{13}$C]palmitate or [1-1$^{14}$C]leucine, respectively; $\text{Rac}_{\text{CO}_2}$ is the rate of appearance of total-body CO$_2$; and $\text{APE}_{\text{S}}$ is the plasma isotopic enrichment of [1-1$^{13}$C]palmitate or [1$^{13}$C]ketoisocaproic acid, respectively, at isotopic equilibrium depending on which substrate oxidation rate is being calculated.

Rates of whole-body protein synthesis were calculated using the equation (Krishnamurti & Janssens, 1988):

\[
\text{Protein synthesis (g/(kg LW)$^{0.75}$ per d)} = \frac{(\text{R}_{\text{leucine}} - \text{leucine oxidation})}{0.081} \times 0.189,
\]

where 0.081 is the average leucine concentration (g/g protein) in cattle carcass protein (Food and Agricultural Organization, 1970), and 0.189 converts from $\mu$mol/min to g/d.

The rate of acetate incorporation into adipose tissue lipid ($R_{\text{lipid}}$) was calculated from the increase in accumulation of $^{14}$C-label in the total lipid over time as described by Greathead et al. (2001).

All rates of metabolism were expressed relative to the animals’ metabolic LW (kg$^{0.75}$).

### Statistical analysis

Data were analysed by multiple linear regression using Genstat for Windows (Release 6.1; Lawes Agricultural Trust, Rothamsted, Hertfordshire, UK). Data were initially fitted to the model:

\[
Y = \alpha + \beta_1 \text{MEI} + \beta_2 \text{Diet} + \beta_3 \text{MEI} \times \text{Diet} + \beta_4 \text{MEI}^2 + \beta_5 \text{MEI}^2 \times \text{Diet},
\]

where $Y$ was the response variable, $\alpha$ was a constant, $\beta_1, \ldots, \beta_5$ were regression coefficients, MEI and MEI$^2$ were the explanatory variables and Diet was the indicator variable. As the quadratic terms MEI$^2$ and MEI$^2 \times \text{Diet}$, and the linear interaction term MEI$\times$Diet, did not improve the fit of the model they were excluded from the final model. However, the $P$ values for the linear interaction term MEI$\times$Diet, when included in the model, are presented for the purpose of illustrating the lack of a differential dietary response to MEI. Residuals were examined for homogeneity of variance and normality. As actual MEI differed from the planned MEI, the fitted model was used to predict responses at the planned levels of MEI, and comparisons between the two diets at the planned MEI were made by $t$ test using the standard errors for the predicted response values and the residual degrees of freedom from the regression.

### Results

#### Chemical composition of the silage and dried grass

The silage composition data presented (Table 2) are the average composition for all bales used. The silage had a DM content of 282.9 g/kg fresh weight and a total N content of 33.5 g/kg DM, of which 10.8% was NH$_3$-N. The iso- and n-butyric acid contents were low at 0.27 and 0.29 g/kg DM, respectively. Lactic acid (50.6 g/kg DM) content was low whilst acetic acid (26.7 g/kg DM) content was considered to be relatively high. On the basis of these values the silage content of N in the total lipid was somewhat surprising, as temperate grasses, unlike tropical grasses, are believed to not accumulate starches (McDonald et al. 1991). This result

### Table 1. Constants ($\alpha$) and coefficients ($\beta$) from the regression of carcass weight (kg) and the chemical components (kg) of the carcass v. live weight (kg) of the initial slaughter group of steers (Mean values with their standard errors)

<table>
<thead>
<tr>
<th></th>
<th>$\alpha$</th>
<th>$\beta$</th>
<th>$\text{RSD}$</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean SE</td>
<td>Mean SE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carcass weight</td>
<td>4.4 0.70</td>
<td>0.46 0.074</td>
<td>0.88 1.68</td>
<td></td>
</tr>
<tr>
<td>Crude protein</td>
<td>0.2 0.21</td>
<td>0.10 0.023</td>
<td>0.77 0.53</td>
<td></td>
</tr>
<tr>
<td>Fat</td>
<td>3.1 1.09</td>
<td>0.07 0.011</td>
<td>0.87 0.26</td>
<td></td>
</tr>
<tr>
<td>Ash</td>
<td>0.7 0.479</td>
<td>0.02 0.005</td>
<td>0.81 0.11</td>
<td></td>
</tr>
<tr>
<td>Water</td>
<td>6.6 4.90</td>
<td>0.28 0.052</td>
<td>0.85 1.16</td>
<td></td>
</tr>
</tbody>
</table>

RSD, residual standard deviation. For details of animals and procedures, see p. 28.
is likely to be indicative of contamination with water-soluble carbohydrates.

**Dietary intakes**

The experiment was designed to provide silage or dried grass to animals over a range of, and where possible, equivalent MEI, from 1·1 × ME\textsubscript{M} to \textit{ad libitum}. The average recorded MEI of the animals in the different treatment groups closely matched the planned MEI levels, with the exception of the \textit{ad libitum} MEI levels, where intakes were more variable (Table 3).

As the concentration of ME in the silage was approximately 0·96 that of the dried grass (Table 2), animals were fed proportionately less dried grass DM than animals fed silage at equivalent levels of MEI. Consequently, animals fed silage had higher \((P<0.001)\) recorded total N intakes than animals fed dried grass at equivalent levels of MEI. However, animals fed dried grass had approximately 85\% higher intakes of insoluble N than animals fed silage at equivalent levels of MEI. Water-soluble carbohydrate intakes for the silage diets were only approximately 8\% of those for the dried grass diets at equivalent levels of MEI. Therefore, over the MEI range of 1·1–1·5 × ME\textsubscript{M}, intakes of insoluble N and water-soluble carbohydrate differed markedly.

At \textit{ad libitum} levels of intake there was no difference \((P>0.05)\) in the mean recorded DM intake between the two diets.
**Table 4. Constants (α) and coefficients (β) from the regression of performance data of steers fed either silage or dried grass v. metabolisable energy intake (MEI)**

(Mean values with their standard errors)

<table>
<thead>
<tr>
<th></th>
<th>Dried grass</th>
<th>Silage</th>
<th>β</th>
<th>RSD (21 df)</th>
<th>MEI</th>
<th>Diet</th>
<th>MEI·Diet*†</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Weights at slaughter</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LW (kg)†</td>
<td>57.7</td>
<td>14.0</td>
<td>54.0</td>
<td>12.8</td>
<td>50.9</td>
<td>9.6</td>
<td>59.9</td>
</tr>
<tr>
<td>Carcass weight (kg)</td>
<td>33.9</td>
<td>7.9</td>
<td>29.7</td>
<td>7.2</td>
<td>23.7</td>
<td>5.4</td>
<td>55.8</td>
</tr>
<tr>
<td>LD (g)</td>
<td>1424</td>
<td>494</td>
<td>1058</td>
<td>449</td>
<td>982</td>
<td>337</td>
<td>46.7</td>
</tr>
<tr>
<td>ST (g)</td>
<td>719</td>
<td>182</td>
<td>529</td>
<td>166</td>
<td>250</td>
<td>124</td>
<td>48.8</td>
</tr>
<tr>
<td>KKCF (g)</td>
<td>−905</td>
<td>242</td>
<td>−759</td>
<td>221</td>
<td>1124</td>
<td>165</td>
<td>65.8</td>
</tr>
<tr>
<td>Daily gains (g/d)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LW</td>
<td>−320</td>
<td>96</td>
<td>−371</td>
<td>87</td>
<td>531</td>
<td>66</td>
<td>79.0</td>
</tr>
<tr>
<td>Carcass weight</td>
<td>−168</td>
<td>61</td>
<td>−229</td>
<td>55</td>
<td>281</td>
<td>41</td>
<td>77.9</td>
</tr>
<tr>
<td>Carcass CP</td>
<td>−20.2</td>
<td>13.1</td>
<td>−37.9</td>
<td>11.9</td>
<td>51.2</td>
<td>8.9</td>
<td>77.4</td>
</tr>
<tr>
<td>Carcass fat</td>
<td>−60.1</td>
<td>13.6</td>
<td>−57.7</td>
<td>12.4</td>
<td>58.2</td>
<td>9.3</td>
<td>62.4</td>
</tr>
<tr>
<td>Carcass water</td>
<td>−84.3</td>
<td>42.9</td>
<td>−122.9</td>
<td>39.0</td>
<td>161.3</td>
<td>29.2</td>
<td>73.8</td>
</tr>
<tr>
<td>Carcass ash</td>
<td>−2.0</td>
<td>3.4</td>
<td>−0.5</td>
<td>3.1</td>
<td>8.2</td>
<td>2.3</td>
<td>32.2</td>
</tr>
<tr>
<td>Carcass energy (MJ/d)</td>
<td>−2.83</td>
<td>0.75</td>
<td>−3.06</td>
<td>0.68</td>
<td>3.47</td>
<td>0.51</td>
<td>71.3</td>
</tr>
<tr>
<td>Carcass composition at slaughter (g/kg carcass)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CP</td>
<td>209.5</td>
<td>8.1</td>
<td>202.1</td>
<td>7.4</td>
<td>−6.9</td>
<td>5.6</td>
<td>24.8</td>
</tr>
<tr>
<td>Fat</td>
<td>16.0</td>
<td>14.2</td>
<td>30.1</td>
<td>13.0</td>
<td>42.8</td>
<td>9.7</td>
<td>48.2</td>
</tr>
<tr>
<td>Protein</td>
<td>0.06</td>
<td>0.07</td>
<td>0.15</td>
<td>0.06</td>
<td>0.23</td>
<td>0.05</td>
<td>56.4</td>
</tr>
<tr>
<td>Water</td>
<td>712.4</td>
<td>19.2</td>
<td>700.6</td>
<td>17.5</td>
<td>−30.4</td>
<td>13.1</td>
<td>18.8</td>
</tr>
<tr>
<td>Ash</td>
<td>56.3</td>
<td>4.2</td>
<td>62.6</td>
<td>3.8</td>
<td>−7.1</td>
<td>2.9</td>
<td>65.5</td>
</tr>
<tr>
<td>Energy (MJ/kg carcass)</td>
<td>5.50</td>
<td>0.63</td>
<td>5.88</td>
<td>0.57</td>
<td>1.52</td>
<td>0.43</td>
<td>33.3</td>
</tr>
</tbody>
</table>

RSD, residual standard deviation; LW, live weight; LD, longissimus dorsi; ST, semitendinosus; KKCF, kidney knob and channel fats; CP, crude protein.

*The MEI Diet term was not included in the model that generated the rest of the data in this table.

†Final LW was predicted from the rate of LW gain prior to entering metabolism crates using linear regression.

### Animal performance

Daily LW gains and final LW increased ($P<0.001$) with increasing MEI (Table 4). Although not significant ($P=0.083$), animals fed grass silage had lower daily LW gains than animals fed dried grass, although this was not reflected by a dietary difference in final LW. This was not due to a dietary difference in the initial LW of the steers at the start of the experiment (96.0 (SD 7.95) v. 93.0 (SD 6.56) kg for animals fed silage and dried grass, respectively).

Carcass and dissected tissue weights all increased ($P<0.01$) with increasing MEI (Table 4). Animals fed dried grass had significantly ($P=0.002$) higher carcass weight than animals fed silage, resulting in carcasses that contained significantly less crude protein (mean: 193 v. 201 g/kg carcass; $P=0.006$) and water (mean: 661 v. 673 g/kg carcass; $P=0.049$) than the carcasses of animals fed dried grass at equivalent levels of MEI. Despite the fact that there were no dietary differences in the daily rates of carcass fat, ash and energy gain, the carcasses of animals fed grass silage contained significantly more fat:protein ratio than animals fed dried grass at equivalent levels of MEI and, although not significant ($P=0.054$), the KKCF of animals fed grass silage was heavier than that of animals fed dried grass at equivalent levels of MEI (mean: 702 v. 556 g; Fig. 1). However, at ad libitum levels of MEI, animals fed dried grass had significantly ($P<0.001$) more KKCF than animals fed silage (1342 v. 927 g).

Daily gains in carcass protein, fat, water and ash all increased significantly ($P<0.01$) with increasing MEI (Table 4). The response of carcass fat gain to MEI was reflected in carcass fat content, which also increased ($P=0.002$) with increasing MEI. The increasing carcass fat content with increasing MEI presumably occurred at the expense of carcass ash content, which decreased ($P<0.001$) with increasing MEI, and carcass protein and water content, which were not affected by MEI. Daily rates of carcass protein and water gain were significantly ($P<0.001$) lower in animals fed silage, resulting in carcasses that contained significantly less crude protein (mean: 193 v. 201 g/kg carcass; $P=0.006$) and water (mean: 661 v. 673 g/kg carcass; $P=0.049$) than the carcasses of animals fed dried grass at equivalent levels of MEI. Daily rates of carcass fat and protein gain were significantly ($P<0.001$) higher in the carcasses of animals fed dried grass than that of animals fed silage, resulting in carcasses that contained significantly more fat:protein ratio than animals fed dried grass (mean: 86 v. 72 g/kg carcass; $P=0.003$) and ash (mean: 53 v. 47 g/kg carcass; $P<0.001$). The increasing carcass fat and protein composition resulted in animals fed grass silage having significantly ($P<0.001$) more KKCF than animals fed dried grass at equivalent levels of MEI and, although not significant ($P=0.052$), they contained more energy (mean: 7.77 v. 7.44 MJ/kg carcass) than the carcasses of animals fed dried grass at equivalent levels of MEI. The dietary differences in carcass fat and protein composition resulted in animals fed grass silage having significantly ($P<0.001$) greater carcass fat:protein ratio than animals fed dried grass at equivalent levels of MEI (mean: 0.45 v. 0.36; Fig. 1). There were no significant differences ($P>0.05$) in carcass fat and protein contents, and thus in the carcass fat:protein ratio, between animals fed ad libitum on silage and dried grass.

### Metabolism

**Fat metabolism.** There was no effect ($P>0.05$) of diet on any of the rates of whole-body fat metabolism measured, i.e.
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Palmitate entry, palmitate oxidation and glycerol entry, or on plasma concentrations of NEFA and glycerol (Table 5). There was a significant ($P = 0.033$) effect of MEI on the rate of palmitate oxidation, which decreased with increasing MEI. Although not significant ($P = 0.055$), plasma NEFA concentrations decreased with increasing MEI.

Rates of acetate incorporation into total lipid of all three adipose tissue depots measured increased ($P < 0.05$) with increasing MEI (Table 6). The rate of acetate incorporation into the total lipid of perirenal adipose tissue was significantly ($P = 0.007$) greater in animals fed silage than in animals fed dried grass at equivalent levels of MEI (mean: 2.33 v. 0.91 μg acetate/min per g lipid; Fig. 1). However, there was no difference ($P > 0.05$) between animals fed ad libitum on silage and dried grass, and no effect of diet on the rates of acetate incorporation into the total lipid of subcutaneous ($P = 0.484$) and omental ($P = 0.398$) adipose tissue.

**Protein metabolism.** Animals fed dried grass had significantly ($P < 0.001$) higher rates of leucine entry (mean: 10.23 v. 8.37 μmol/min per kg LW$^{0.75}$) and oxidation (mean: 3.00 v. 1.41 μmol/min per kg LW$^{0.75}$) and significantly ($P < 0.001$) higher plasma leucine concentrations.

**Fig. 1.** The relationships between metabolisable energy intake (MEI; £ maintenance) and carcass fat:protein ratio (a), carcass fat (b), protein gain (c), whole-body protein synthesis (d), kidney knob and channel fats weight (KKCF; e) and the rate of acetate incorporation into the total lipid of perirenal adipose tissue (f) in cattle fed grass silage (●) or dried grass (○). Also shown are the lines through the silage (—) and dried grass (---) data from the fitted model $Y = a + b_1 \text{MEI} + b_2 \text{Diet}$, the constants and coefficients of which can be found in Tables 4, 5 and 6. Values are means with the residual standard deviation shown by vertical bars (21 df).
Table 5. Constants ($\alpha$) and coefficients ($\beta$) from the regression of parameters of whole-body metabolism measured in steers fed either silage or dried grass v. metabolisable energy intake (MEI)
(Mean values with their standard errors)

<table>
<thead>
<tr>
<th></th>
<th>Dried grass</th>
<th>Silage</th>
<th>$P$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha$</td>
<td>Mean</td>
<td>SE</td>
<td>Mean</td>
</tr>
<tr>
<td>$RaCO_2$ (\mu mol/min per kg LW$^{0.75}$)</td>
<td>605</td>
<td>238</td>
<td>631</td>
</tr>
<tr>
<td>$RaPalmitate$ (\mu mol/min per kg LW$^{0.75}$)</td>
<td>1.68</td>
<td>0.52</td>
<td>1.75</td>
</tr>
<tr>
<td>$RaGlycerol$ (\mu mol/min per kg LW$^{0.75}$)</td>
<td>0.98</td>
<td>0.34</td>
<td>1.04</td>
</tr>
<tr>
<td>Protein synthesis (g/kg LW$^{0.75}$ per d)</td>
<td>8.73</td>
<td>3.49</td>
<td>9.50</td>
</tr>
<tr>
<td>Plasma NEFA concentration (\mu mol/l)</td>
<td>21.6</td>
<td>55.9</td>
<td>38.6</td>
</tr>
<tr>
<td>Plasma leucine concentration (\mu mol/kg LW$^{0.75}$)</td>
<td>4.91</td>
<td>1.47</td>
<td>3.04</td>
</tr>
<tr>
<td>Plasma insulin concentration (U/ml)</td>
<td>0.96</td>
<td>0.73</td>
<td>-0.63</td>
</tr>
<tr>
<td>Plasma glycerol concentration (\mu mol/kg LW$^{0.75}$)</td>
<td>208.3</td>
<td>56.7</td>
<td>210.0</td>
</tr>
<tr>
<td>Plasma leucine concentration (\mu mol/kg LW$^{0.75}$)</td>
<td>14.0</td>
<td>14.4</td>
<td>14.9</td>
</tr>
<tr>
<td>Plasma acetate concentration (\mu mol/kg LW$^{0.75}$)</td>
<td>181.0</td>
<td>22.9</td>
<td>85.5</td>
</tr>
<tr>
<td>Plasma insulin concentration (U/ml)</td>
<td>627.0</td>
<td>145.0</td>
<td>444.0</td>
</tr>
<tr>
<td> </td>
<td>1.05</td>
<td>3.24</td>
<td>-2.81</td>
</tr>
</tbody>
</table>

RSD, residual standard deviation; $Ra$, entry rate.
†The calculation used to determine $RaCO_2$ did not correct for CO$_2$ sequestered in the body.
For details of diets and procedures, see p. 28.

Table 6. Constants ($\alpha$) and coefficients ($\beta$) from the regression of rates of acetate incorporation into the total lipid ($R_{lipid}$, \mu g acetate/min per g lipid) of different adipose tissue depots of steers fed silage or dried grass v. metabolisable energy intake (MEI)
(Mean values with their standard errors)

<table>
<thead>
<tr>
<th>Depot</th>
<th>Dried grass</th>
<th>Silage</th>
<th>$P$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>Mean</td>
</tr>
<tr>
<td>Subcutaneous</td>
<td>-10.03</td>
<td>2.08</td>
<td>-9.61</td>
</tr>
<tr>
<td>Omental</td>
<td>-7.00</td>
<td>1.47</td>
<td>-6.62</td>
</tr>
<tr>
<td>Perirenal</td>
<td>-3.58</td>
<td>1.61</td>
<td>-2.16</td>
</tr>
</tbody>
</table>

RSD, residual standard deviation.
*The MEI-Diet term was not included in the model that generated the rest of the data in this table.
For details of diets and procedures, see p. 28.

Discussion
The present experiment had two objectives. The first was to determine whether rates of fat accretion in cattle fed grass...
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Silage are higher than in cattle fed dried grass and thus whether this, together with impaired rates of protein accretion, contributes to the high carcass fat:protein ratio of cattle fed grass silage. The second objective was to determine whether or not responses to increasing MEI differ between grass silage and dried grass diets. To fulfil these objectives measures of fat and protein metabolism, using isotope dilution and incorporation techniques, were combined with measures of carcass composition in young growing cattle fed either grass silage or dried grass over a range of equivalent MEI levels.

Before discussing the results for the present experiment there are a number of points relating to the experimental design and methodology worth considering. First, the range of MEI fed was achieved by changing the amount of feed offered rather than by changing the composition of the diet. While this ensured that the proportion of nutrients in the diet remained unchanged, it did mean that MEI was not the only dietary component changed, and thus intake effects were not limited to ME. Second, the experiment relied on the assumption that metabolism, measured in animals confined to metabolism crates and fed hourly, reflects that responsible for carcass composition, which would have been largely defined by the growth period outside metabolism crates, during which time they were fed twice daily. It is acknowledged that the direct relevance of metabolism measurements made on hourly fed animals in practical production systems could be challenged (Thorp et al. 2000).

Carcass composition

The experiment confirmed that the carcasses of cattle fed grass silage do indeed have a high carcass fat:protein ratio. This was shown to be true when carcass fat:protein ratios of cattle fed grass silage were compared with those fed dried grass at equivalent levels of MEI. Interestingly, there was no difference in carcass fat:protein ratio between animals fed ad libitum on the two diets. This was attributable to the combined effects of the increase in fat:protein ratio with increasing MEI (Table 4) and the greater MEI of animals fed ad libitum on dried grass compared with grass silage (Table 3). This result may provide a plausible explanation as to why in some comparative carcass composition experiments, involving cattle fed grass silage and dried grass-based diets, no differences in carcass fat content have been reported, as these experiments did not use diets formulated to be isoenergetic (Steen & Moore, 1988, 1989; Steen, 1991). Studies that have reported differences in carcass fat content between cattle fed silage-based diets and dried forage-based diets have all fed isoenergetic diets (Lonsdale, 1976; Moore & Steen, 1983; Steen, 1991).

Protein metabolism

Clearly, a high carcass fat:protein ratio can be the result of a limited rate of protein deposition, an increased rate of fat deposition, or a combination of both. That protein deposition is limited in cattle fed grass silage is well established (Gill et al. 1987), and the performance data (Table 4) from the present experiment clearly support this, with cattle fed grass silage having lower daily carcass protein gains than cattle fed dried grass. However, there was no difference in rates of whole-body protein synthesis between the diets. If it is assumed that skeletal muscle accounts for a fixed proportion of whole-body protein synthesis, e.g. 20% (Lobley, 1993), irrespective of diet and level of MEI, and that carcass protein is predominantly associated with skeletal muscle, then the ratio of carcass protein gain:synthesis in cattle fed grass silage was lower than that for cattle fed dried grass (0·24 (SD 0·06) v. 0·39 (SD 0·09), respectively; \( P < 0·001 \)), i.e. rates of carcass protein turnover were greater in cattle fed grass silage. However, this is unlikely as turnover rates are normally positively associated protein accretion rates (Lobley et al. 1987), and thus one would expect turnover rates to be greatest for the dried grass diet. In any case, where animals are fed different diets and at different levels of MEI, the assumption that skeletal muscle accounts for a fixed proportion of whole-body protein synthesis would be inappropriate. It has been suggested that a relationship between dietary fibre content and gut protein turnover exists (Seal & Parker, 2000). While there was little difference in neutral detergent fibre concentration between the two diets, the grass silage contained approximately 6% more acid detergent fibre. It is therefore possible that gut protein turnover in cattle fed grass silage accounted for a larger proportion of the whole-body protein synthesis than in cattle fed the dried grass. Based on the current understanding of the problem, i.e. the limited protein deposition in cattle fed grass silage, it was hypothesised that cattle fed grass silage would have had lower rates of whole-body protein synthesis. This is because amino acid intake and rates of protein synthesis have been shown to be positively related (Reeds & Davis, 1992) – in cattle fed grass silage flows of duodenal amino acids have been shown to be limiting (Baker et al. 1985; Gill et al. 1987; Thomas & Gill, 1988; Veira et al. 1994). Based on the lack of a dietary difference in the rate of whole-body protein synthesis, it might therefore be concluded that in the present experiment duodenal flows of amino acids were similar for the two diets. This is unlikely though, as the greater leucine entry and oxidation rates, and greater plasma leucine concentrations of animals fed dried grass (Table 5), are indicative of greater leucine absorption on this diet, as these parameters have been shown to be a function of intake (Meguid et al. 1986; Hammond et al. 1987; Lapierre et al. 2002; Savary-Auzeloux et al. 2003). This is supported by the effect of MEI, and thus protein intake as the relative composition of the diets remained unchanged, on these parameters associated with whole-body protein metabolism.

Based on the evidence of previous reports and the evidence of the present experiment, the limited rates of carcass protein gain, the lower plasma leucine concentration and the lower leucine entry and oxidation rates of cattle fed grass silage, it therefore seems likely that the result for rates of whole-body protein synthesis is misleading through failure to reveal a dietary difference. Based on the residual standard deviation (2·101) and degrees-of-freedom (21) for rates of protein synthesis (Table 5), it can be calculated that the least significant difference (\( P = 0·05 \)) between two means required would have been 1·78 g/kg LW\(^{0·75} \) per d, i.e. a 10-5% difference. Where differences as small as 0·1% in the ratio of protein synthesis can effect rates of tissue protein gains of 20–100% (Lobley, 1993), the sensitivity of the isotope dilution technique as used to measure rates of whole-body protein synthesis rates is clearly inadequate.
Fat metabolism

Evidence to support the hypothesis that rates of fat accretion in cattle fed grass are elevated and thus contribute to the high carcass fat:protein ratios was inconclusive. There was no difference in the rate of carcass fat gain between animals fed grass silage and dried grass. The lack of a dietary difference in the rate of lipogenesis in adipose tissue from the subcutaneous depot, a depot associated with the carcass, corroborates this result. Thus, the higher concentration of carcass fat in cattle fed grass silage would appear to be due to the effect of the reduced rates of protein and water accretion on the proportions of the carcass constituents measured. The fact that young, growing animals were used in this experiment, combined with their overall relatively poor rates of LW gain (Table 4), could explain the lack of a dietary effect on rates of carcass fat gain. However, the reason for using young, growing animals was that it was in similarly aged animals that Lonsdale (1976) reported differences in carcass composition. Also, if rates of fat deposition were elevated in young animals then this could have important implications on animal mature size (Owens et al. 1993).

However, the experiment does provide evidence for elevated rates of fat accretion in non-carcass fat depots. There was a trend ($P=0.054$) for cattle fed grass silage to have more KKCF than cattle fed dried grass, a result given credence by the higher rates of lipogenesis measured in adipose tissue from the perirenal depot. As for protein accretion, fat accretion is dependent upon the relative rates of lipogenesis and lipolysis and therefore an increase in the rate of lipogenesis does not necessarily infer an increase in the rate of fat accretion. However, the fact that there was this trend for a dietary difference in the KKCF weight, and that there was no difference in the rate of glycerol appearance, an index of lipolysis, suggest that the difference is indicative of an increased rate of fat accretion in this depot. Lonsdale (1976) similarly reported that dietary differences (silage v. silage plus dried grass diets) in fat deposition appeared to be more marked in non-carcass than carcass components in young cattle (approximately 110 kg LW at slaughter).

It is possible that the result is a function of depot activity, depot activity being related to the stage of animal maturity. Carcass fat depots have been shown to be late-developing relative to non-carcass depots (Cianzio et al. 1985; Scollan et al. 2003). Therefore, it is tempting to speculate that had the animals been allowed to advance in maturity before slaughter, dietary differences in rates of carcass fat accretion may have been observed as they were for the perirenal depot.

Lonsdale (1976) proposed that elevated rates of fat accretion in cattle fed grass silage are the result of a limiting supply of amino acids for protein synthesis on this diet, with the consequent increase in energy available above maintenance stored as fat. This has been supported by experiments where reductions in carcass fat content have been achieved in cattle fed grass silage by increasing the duodenal supply of amino acids, through supplementation (Baker et al. 1985, 1992) and formaldehyde treatment (Thompson et al. 1981).

The principal energy substrate in ruminants is acetate. Animals fed grass silage had lower plasma concentrations of acetate than animals fed dried grass. Differences in circulating acetate concentrations normally arise through differences in rumen (Pethick et al. 1981) and endogenous acetate production (Cronjé et al. 1991). There was no dietary difference in acetate entry rate, yet animals fed grass silage had lower plasma acetate concentrations. This implies that animals fed grass silage had greater clearance rates (acetate disappearance rate, which under ‘steady-state’ conditions is assumed to equal acetate entry rate divided by plasma acetate concentration) of acetate than animals fed dried grass (239 (SD 61) v. 185 (SD 28) ml/min per kg LW$^{0.75}$, respectively; $P<0.01$). However, there is no obvious explanation for this.

Insulin

Hormones are important mediators of the effect of diet on growth and development. In the present experiment plasma insulin concentrations were measured. The increase in plasma insulin concentration with increasing MEI is consistent with the understanding that insulin status in ruminants is regulated by energy and amino acid supply (Lobley, 1992). The fact that animals fed dried grass had higher concentrations of insulin than animals fed grass silage at equivalent levels of MEI could indicate that there was a dietary difference in the duodenal supply of amino acids in the present study, as discussed earlier, although insulin release is believed to be more affected by propionate than amino acid absorption (Mineo et al. 1994; Gonda et al. 1997).

There was a significant correlation between plasma insulin concentration and both carcass protein gain ($r=0.722, P<0.001$) and carcass fat gain ($r=0.475, P<0.05$), which is consistent with insulin’s role as a modulator of feed induced anabolic activity. Breier & Gluckman (1991) suggested that the importance of insulin as a regulator of growth may be increased when nutrients for growth are limiting. In the present experiment there was no evidence of an effect of MEI on the significance of the correlation between insulin and carcass protein and fat gain. The strength of the correlation with carcass protein gain might suggest a greater role for insulin in directing protein metabolism than for fat metabolism. This suggestion is supported by the higher plasma insulin concentrations in animals fed dried grass, which had higher rates of protein gain than animals fed grass silage. Thorp et al. (2000) reported higher plasma insulin concentrations in cattle fed grass silage supplemented with barley, diets for which the group had previously reported reduced carcass fat:protein ratios, than cattle fed unsupplemented silage. Indeed, the role of insulin in directing fat metabolism in ruminants is uncertain; for example, Smith et al. (1992) were unable to demonstrate a correlation between insulin and fatty acid synthesis in vitro, while Mills et al. (1989) were able to.

The importance of the growth hormone/insulin-like growth factor I (IGF-I) axis as a major factor controlling postnatal growth and its interaction with nutritional status is well documented. Plasma growth hormone and IGF-I concentrations were not measured in the present experiment. However, circulating insulin concentrations have been shown to broadly correlate with circulating IGF-I concentrations (Dawson et al. 1998), and thus it is logical to speculate that animals fed dried grass might have had higher plasma IGF-I concentrations. IGF-I production is believed to be associated with the hepatic response to growth hormone, an association modulated by nutritional status (Brameld et al. 1996) and insulin.
in vivo reported no differences in the relative rates of the animal’s stage of maturity, as mentioned earlier, but also by specific metabolic activity is not only determined by the affects of MEI (Table 6). At low MEI acetate incorporation into perirenal adipose tissue were in part mediated by this hormone.

Metabolisable energy intake

The objective of feeding diets over a range of MEI was to determine whether there was an interaction between form of ME, grass silage v. dried grass, and quantity of ME, 1 × MEin to ad libitum, both of which are considered important determinants of animal performance (Beever et al. 1988; Thomas & Gill, 1988; Steen, 1992; Steen & Robson, 1995). As the overall efficiency of energy (Thomas & Chamberlain, 1990) and amino acid (Beever et al. 1992; MacRae et al. 1995) utilisation of animals fed grass silage is considered to be poor, it was hypothesised that animals fed the different diets would respond differentially to changes in MEI. However, the lack of an interaction between diet and MEI for any of the parameters measured refutes this hypothesis. The fact that the ratio of dietary components remained constant irrespective of MEI may explain this result, as the inefficiencies in nutrient utilisation have been related to imbalances in nutrient supply (Beever et al. 1992).

The fact that linear regression best described the response to MEI for all the parameters measured indicates that there was no threshold requirement for MEI below which responsiveness was minimal. This is contrary to what has been reported by Smith et al. (1992), who did demonstrate the presence of a threshold requirement for MEI for in vitro adipose tissue anaerobic activities, but not for in vivo measures of N metabolism. However, their range of MEI did include below maintenance requirement levels of MEI, whereas the present experiment did not.

With regard to the rates of acetate incorporation into the total lipid of subcutaneous, omental and perirenal adipose tissue per se, there did appear to be a differential response to MEI (Table 6). At low MEI acetate incorporation into lipid was greatest in perirenal adipose tissue, whereas at high intakes the greatest rates of acetate incorporation into lipid were measured in subcutaneous adipose tissue. Rates of acetate incorporation into the omental adipose tissue were low to intermediate at all levels of intake. This would imply that when nutrient supply is limiting non-carcass depots are favoured over carcass depots; in other words, that depot-specific metabolic activity is not only determined by the animal’s stage of maturity, as mentioned earlier, but also by levels of nutrient supply. However, Broad & Ulyatt (1980) reported no differences in the relative rates of in vivo lipogenic activity between depots in sheep fed at maintenance, 1 × maintenance and ad libitum.

Summary

From the results of the present study it was concluded that the high carcass fat:protein ratios of young growing steers is the result of limited rates of protein accretion. While there was evidence that rates of non-carcass fat accretion were elevated in cattle fed grass silage, there was no evidence to support the hypothesis that, in cattle of the age used in the present experiment, elevated rates of carcass fat accretion contribute to the high carcass fat:protein ratio. The lack of any interaction between diet and MEI suggests that the efficiency of ME utilisation is dependent upon form, form including the source of the ME and ratio of ME relative to the other dietary components, rather than quantity.

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References


