Effects of diet forage proportion on maintenance energy requirement and the efficiency of metabolizable energy use for lactation by lactating dairy cows

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ABSTRACT

The objective of the present study was to examine the effect of dietary forage proportion (FP) on metabolizable energy (ME) requirement for maintenance (ME_m) and the efficiency of ME use for lactation (k_l) in lactating dairy cows. Data used were derived from 32 calorimetric chamber experiments undertaken at our institute between 1992 and 2010, including data from 818 Holstein-Friesian cows (HF), 50 Norwegian Red cows, and 62 crossbred cows (Jersey $\times$ HF or Norwegian Red $\times$ HF). Animals were offered forage-only rations ($n = 66$) or forage and concentrate rations ($n = 864$) with FP ranging from 18 to 100% (dry matter basis). The effect of FP was evaluated by dividing the whole data set into 4 groups according to the FP ranges, categorized as FP <30%, FP = 30 to 59%, FP = 60 to 99%, and FP = 100%. The ME_m for individual cows was calculated from heat production minus energy losses from inefficiencies of ME use for lactation, energy retention and pregnancy, and k_l was obtained from milk energy output adjusted to zero energy balance ($E_{l(0)}$) divided by ME available for production. Increasing FP significantly reduced ME intake and milk energy output, although the differences between the 2 low FP groups were not significant. However, increasing FP significantly increased the ratio of heat production over ME intake and ME_m ($MJ/kg^{0.75}$), with the exception that the increases did not reach significance in heat production/ME intake between FP <30% and FP = 30 to 59%, or in ME_m between FP = 60 to 99% and FP = 100%. However, the FP had no significant effect on the k_l values, which were similar among the 4 groups of cows. The effect of FP was also evaluated using the linear mixed regression technique relating $E_{l(0)}$ to ME intake. The results demonstrated that with a common

regression coefficient (slope), the regression constants (intercepts) taken as net energy requirement for maintenance significantly increased with increasing FP. However, the increase between the 2 high FP groups did not reach research significance. It is concluded that increasing diet FP had no effects on k_l but significantly increased maintenance energy requirement ($MJ/kg^{0.75}$). These results indicate that using the current energy feeding systems to ration dairy cows managed under low input systems may underestimate their nutrient requirements, because the majority of feeding systems adopted globally do not differentiate the maintenance energy requirements between low and high forage input systems.

Key words: forage proportion, maintenance energy requirement, energy utilization efficiency, lactating dairy cow

INTRODUCTION

Low-input dairy farming is widely adopted in favorable grass-growing areas of the world (e.g., in New Zealand, Australia, and Ireland) or in countries where the economic conditions constrain high-concentrate inputs (e.g., in some developing countries). These low-input systems are increasingly recognized as delivering multi-functional benefits to the agricultural industry and society, in contrast to some higher input systems, which are often linked with fertility, health, and welfare challenges (Seykora and McDaniel, 1983; Ingvarsen et al., 2003; König et al., 2008; Koeck et al., 2014). Dairy cows managed under the low-input systems are normally offered forage-based diets supplemented with no or a small amount of concentrates. However, forages are bulky materials and normally contain less ME than concentrate supplements, although high-quality grass may have a comparable ME concentration to that of concentrates. Therefore, cows offered forage-based diets may need to consume a greater physical quantity of bulky forages than those offered concentrate-based di-

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ets to achieve a given level of ME intake. However, evidence indicates that high intakes of bulky forage could increase maintenance metabolic rates of cows (Dong et al., 2015). The greater physical intake required with a forage-based diet to achieve similar levels of ME intake are likely to result in greater gut fill, an increased energy expenditure on rumination and digestion, and a greater production of acetic acid in the rumen. All of these factors can contribute to an increase in gut mass, an increase in the size of other internal organs (Reynolds, 1996), and a higher metabolic rate. The protein metabolism in gut, liver, and other internal organs can produce much more heat per unit of weight than that of muscle (Baldwin et al., 1985; Johnson et al., 1990). Indeed, an earlier calorimeter chamber study involving lactating dairy cows found that ME requirement for maintenance (ME_m) increased from 0.59, 0.68, to 0.74 MJ/kg^{0.75} when cows were offered diets containing forage levels of less than 50%, 50 to 99%, and 100% (Yan et al., 1997). However, energy rationing systems for dairy cows currently adopted in North America and Europe do not consider the effects of diet forage proportion on basal metabolic rates. Indeed, many of these systems were developed using data from animals offered diets with a low forage proportion (FP). Using these systems to ration dairy cows managed within systems with a high FP may result in an underestimation of their maintenance energy requirement.

In recognition of the need to optimize the competitiveness of low-input and organic dairy farming, the European Union funded a research project in 2012 to evaluate measures to improve the efficiency and welfare of animals within low-input and organic dairy systems. The present study was part of this project and was designed to address the knowledge gap described previously. Therefore, the objectives of the present study were to use a large calorimeter data set of lactating dairy cows collated at this institute to investigate the influence of diet FP on energetic efficiency, and to quantify any differences in ME_m and the efficiency of ME use for lactation (k_l) for lactating dairy cows offered diets containing low and high proportions of forage.

MATERIALS AND METHODS

Animals and Diets

Data used were collated from 32 individual experiments involving lactating dairy cows undertaken at this institute from 1992 to 2010, including data from 818 Holstein-Friesian cows (HF), 50 Norwegian Red cows, and 62 crossbred cows (Jersey × HF or Norwegian Red × HF, F₁ hybrid). The majority of these studies have

been published in peer-reviewed scientific journals, and their references are presented in the Appendix. The HF cows had a range of Profitable Lifetime Index (£) from −93 to 145, based on the calculation of Predicted Transmitting Ability 2010 proof under the UK genetic evaluation system. The crossbred animals were the offspring of a crossbreeding program undertaken within the Agri-Food and Biosciences Institute Hillsborough herd. The cows were at different stages of lactation when housed in the calorimeter chambers, with a mean DIM of 159 for HF cows, 158 for Norwegian Red cows, 179 for Jersey × HF cows, and 247 for Norwegian Red × HF cows. Parity of the cows was as follows: 258 first parity, 206 second parity, and 466 between parities 3 and 9.

All diets were offered *ad libitum*, with cows offered either forage-only diets (n = 66), or a mixture of forage and concentrates (n = 864), according to protocols within individual experiments. The forages offered included grass silage (n = 623), mixtures of grass silage and maize silage (n = 155), mixtures of grass silage and whole crop wheat silage (n = 4), mixtures of fresh grass and straw (n = 4), maize silage (n = 6), whole crop wheat silage (n = 6), straw (n = 36), fresh grass (n = 42), dried grass (n = 20), and dried lucerne (n = 34). The grass silages were produced from primary growth, primary regrowth, and secondary regrowth material, with grass either unwilted or wilted before ensiling, and ensiled with or without application of silage additives. Grass (fresh and dried) and grass silages offered were produced from predominantly perennial ryegrass swards containing a range of varieties (e.g., Aberstar, Aberzest, Fetione, Magella, Menna, Merbo, Merlinda, and Spelga). The concentrates offered included a mineral-vitamin supplement and some of the following ingredients: cereal grains (barley, wheat, or maize), by-products (maize gluten meal, molassed or unmolassed sugar-beet pulp, citrus pulp, or molasses), and protein feeds (soybean meal or rapeseed meal). Diets were either 100% forage (n = 66) or contained varying proportions of concentrate, from 13 to 82% (n = 864).

Digestibility and Calorimeter Measurements

Energy intake and output data used in the present study were measured in digestibility trials and by indirect open-circuit respiration calorimeter chambers. Before the commencement of nutrient utilization measurements, all dairy cows were offered their experimental diets for at least 3 wk in group-housed cubicle accommodation with free access to water. Afterward, animals were transferred to a tie-stall facility and remained in individual stalls for between 5 to 8 d, with

measurement of total feed intake and total collection of feces and urine undertaken during the final 3 to 6 d. Faces and urine outputs were recorded and sampled daily as a proportion (15%) of total excretion of faces (by weight) and urine (by volume). To prevent loss of N as ammonia, sulfuric acid (35% H₂SO₄) was added to containers used to collect urine (10 to 35 mL/container with a target to maintain the pH value of urine under 3). Immediately after the completion of digestibility measurements, animals were then housed in calorimeter chambers for 3 to 5 d with measurement of gaseous exchange (CH₄, CO₂, and O₂) taking place during the final 2 to 4 d. All equipment, sampling procedures, analytical methods, and calculations used in the calorimetric studies were described by Gordon et al. (1995), and calibration of the chambers by Yan et al. (2000).

Calculation of Maintenance Energy Requirement and the Efficiency of ME Use for Lactation

The ME_m (MJ/d) for individual cows was estimated from heat production (HP, MJ/d) minus energy losses from the inefficiencies of ME use for lactation, tissue change, and pregnancy (equations 1 and 2), with HP, milk energy output (E_l, MJ/d), and tissue energy change (E_g, MJ/d) measured in the present study and energy for pregnancy (E_p, MJ/d) estimated using models of Agricultural and Food Research Council (AFRC, 1993).

$$\text{If } E_g < 0, \text{ ME}_m = \text{HP} - (1/k_{l(\text{AFRC})} - 1) \times E_l - (1/k_t - 1) \times E_g - (1/k_p - 1) \times E_p, \text{ or} \quad [1]$$

$$\text{if } E_g > 0, \text{ ME}_m = \text{HP} - (1/k_{l(\text{AFRC})} - 1) \times E_l - (1/k_g - 1) \times E_g - (1/k_p - 1) \times E_p, \quad [2]$$

where $k_{l(\text{AFRC})}$ is the efficiency of ME use for lactation ($= 0.35\text{ME}/\text{GE} + 0.42$; AFRC, 1993), k_g is the efficiency of ME use for weight gain ($= 0.95 \times k_{l(\text{AFRC})}$), k_t is the efficiency of utilization of mobilized tissue energy for lactation ($= 0.84$), and k_p is the efficiency of ME use for pregnancy ($= 0.133$). All these efficiencies are from the recommendation of AFRC (1993). The E_p (MJ/d) was calculated using equations 3 and 4 (AFRC, 1993)

$$\log_{10}(E_t) = 151.665 - 151.64 \times e^{-0.0000576t}, \quad [3]$$

$$E_p = 0.025 \times W_c \times (E_t \times 0.0201e^{-0.0000576t}), \quad [4]$$

where E_t is total energy retention (MJ), W_c is calf birth weight, and t is days from conception.

The k_l for individual cows used in the present study was calculated as

$$k_l = E_{l(0)} / (\text{ME intake} - \text{ME}_m), \quad [5]$$

where ME_m (MJ/d) was derived from equation 1 or 2, and E_{l(0)} is milk energy output adjusted to zero energy balance (MJ/d) and was calculated from equations 6 and 7 (AFRC, 1993):

$$\text{if } E_g > 0, E_{l(0)} = E_l + (1/0.95) \times E_g; \quad [6]$$

$$\text{if } E_g < 0, E_{l(0)} = E_l + 0.84 \times E_g. \quad [7]$$

Statistical Analysis

The effect of dietary FP on energy expenditure and energetic efficiency of lactating dairy cows was evaluated using 2 analytical approaches: ANOVA and linear mixed regression technique. To facilitate the statistical analysis, the whole data set was divided into 4 groups based on diet FP data, categorized as FP <30% ($n = 145$), FP = 30 to 59% ($n = 478$), FP = 60 to 99% ($n = 241$), and FP = 100% ($n = 66$) groups. All analyses were carried out using the GenStat program (16.2; Payne et al., 2013).

ANOVA

The ANOVA procedure was undertaken with the 4 FP groups fitted as a fixed effect and experiment and animal within experiment fitted as random effects in all models. Additional combinations of the covariates, when appropriate, were also fitted as supplementary fixed effects for evaluation of energetic efficiencies, which included breed, parity, days in milk, days pregnant, and dietary contents of ME, CP, and NDF. The significance or otherwise of the fixed effects was assessed by comparing a Wald statistic against the appropriate F -distribution. If any of the additional fixed effects was not significant ($P > 0.05$), then it was removed from the analyses in equations and the model was refitted.

Linear Mixed Regression

Linear relationships between E_{l(0)} and ME intake or between HP and ME intake were developed for each group and compared to identify the presence of any significant difference among the 4 constants (intercepts) with a common regression coefficient (slope) using the 4 groups of FP data, as described previously. The constant (intercept) obtained from the relationship between E_{l(0)} (MJ/kg^{0.75}) and ME intake (MJ/kg^{0.75})

is taken as the NE_M (AFRC, 1993). Experiment and animal-within-experiment were fitted as random effects in all models, whereas the explanatory variable was treated as a fixed effect. Additional combinations of the covariates, when appropriate, were also fitted as supplementary fixed effects for evaluation of energetic efficiencies, which included breed, parity, days in milk, days pregnant, and dietary contents of ME, CP, and NDF. The significance or otherwise of the fixed effects was assessed by comparing a Wald statistic against the appropriate F -distribution. If any of the additional fixed effects was not significant ($P > 0.05$), then it was removed from the analyses and the model was refitted. For regressions obtained from each of the 4 groups, pair-wise differences between the different intercepts and slopes were also calculated if the main effect was significant, using Fisher's least significant difference test. Finally an assessment of the goodness-of-fit of each model was made by calculating a pseudo R^2 value (calculated in each case as the square of the correlation of the fitted values from the model with the observed values for the response variable).

RESULTS

The animal, diet, and energy metabolism data used in the present study are presented in Table 1. The data set had a large range in BW (379 to 757 kg), BCS (1.5 to 4.5), DIM (18 to 307), and lactation number (1.0 to 9.0). The cows used were offered either forage-only diets or mixed diets, representing various FP (0.18 to 1.00 kg/kg of DM) and fiber contents (NDF = 0.215 to 0.598 kg/kg of DM and ADF = 0.110 to 0.436 kg/kg

of DM). The mean data for the 4 groups of data (FP < 30%, 30–59%, 60–99%, and 100%) are, respectively, NDF (kg/kg of DM) of 0.229, 0.211, 0.248, and 0.308; and ADF (kg/kg of DM) of 0.396, 0.375, 0.429, and 0.542.

The analysis (ANOVA) of effects of FP on animal, diet, and energy metabolism variables are presented in Table 2. As expected, increasing diet FP significantly reduced DMI, BW, and energy-corrected milk yield (ECMY; $P < 0.001$), although the difference was not significant in BW between FP = 30 to 59% and FP = 60 to 99%, or in DMI or ECMY between the 2 low FP groups. No significant difference was found in ME intake, HP, or E_l between the 2 low FP groups, and these 3 variables decreased significantly with increasing diet FP from 30 to 59% to 100% ($P < 0.001$). The FP = 100% group had a significantly lower ME/GE and ME/DE than the other 3 groups ($P < 0.001$). Increasing diet FP significantly increased HP/ME intake, and reduced E_l /ME intake ($P < 0.001$), with the exception that the differences between the 2 low FP groups did not reach significance. The ME_m ($MJ/kg^{0.75}$) increased significantly with increasing diet FP ($P < 0.001$), although the increase between the 2 high FP groups was not significant. However, FP had no significant effect on k_l , which was similar among the 4 groups of cows.

The contribution of diet FP to the variation in energy expenditure was further investigated using the linear regression between $E_{l(0)}$ or HP and ME intake among the 4 groups of cows. The results are presented in Table 3 and Figures 1 and 2. Using the linear mixed regression technique, a common coefficient was developed for the relationship between $E_{l(0)}$ and ME intake (equations

Table 1. Animal, diet, and energy metabolism data used in the present study

Item	Mean	SD	Minimum	Maximum
Animal and dietary data				
BW (kg)	553	66.7	379	757
BCS	2.5	0.39	1.5	4.5
DIM	164	85.9	18	307
Lactation number	2.5	1.6	1	9
DMI (kg/d)	16.9	3.41	6.0	26.6
Milk yield (kg/d)	22.4	7.83	3.2	49.1
CP content (kg/kg of DM)	0.178	0.0295	0.112	0.262
ADF content (kg/kg of DM)	0.230	0.0520	0.110	0.436
NDF content (kg/kg of DM)	0.408	0.0942	0.215	0.598
Forage proportion (kg/kg of DM)	0.533	0.2041	0.180	1.000
Energy intake and output data (MJ/d)				
Gross energy intake	311	63.3	114	485
Fecal energy	79	21.1	25	150
Urinary energy	11	4.1	2	59
Methane energy	21	4.4	8	38
Heat production	125	20.3	67	184
Milk energy	70	23.2	3	141
Energy balance	4	22.8	−88	71

Table 2. Comparison of animal, diet, and energy metabolism data among the 4 forage proportion groups¹

Item	Forage proportion (%)				SED	P-value
	<30	30–59	60–99	100		
Animal and dietary data						
BW (kg)	602 ^a	582 ^b	575 ^b	553 ^c	11.9	***
BCS	2.59	2.59	2.49	2.5	0.130	NS
DMI (kg/d)	17.4 ^a	18.0 ^a	15.9 ^b	13.9 ^c	1.0	***
ECMY (kg/d)	25.1 ^a	24.2 ^a	17.7 ^b	13.3 ^c	0.89	***
Energy intake and output data (MJ/d)						
ME intake	208 ^a	211 ^a	181 ^b	153 ^c	13.8	***
Heat production	128 ^a	132 ^a	120 ^b	109 ^c	6.8	***
Milk energy	79 ^a	75 ^a	60 ^b	44 ^c	6.3	***
Energy balance	1.6	3	2	2.3	6.0	NS
Energy utilization data						
DE/GE	0.748	0.739	0.737	0.698	0.0205	NS
ME/GE	0.645 ^a	0.637 ^a	0.628 ^a	0.586 ^b	0.0176	***
ME/DE	0.858 ^a	0.854 ^a	0.853 ^a	0.838 ^b	0.0083	***
Heat production/ME intake	0.629 ^c	0.635 ^c	0.669 ^b	0.727 ^a	0.0240	***
Milk energy/ME intake	0.382 ^a	0.368 ^a	0.332 ^b	0.282 ^c	0.0255	***
Energy balance/ME intake	0.007	0.016	0.009	0.022	0.0195	NS
ME _m (MJ/kg ^{0.75})	0.608 ^c	0.653 ^b	0.673 ^a	0.676 ^a	0.0171	***
k _l	0.638	0.644	0.634	0.629	0.0023	NS

^{a–c}Means with the same superscript letter in the same row are not significantly different ($P > 0.05$).

¹SED = standard error of difference; ECMY = energy-corrected milk yield; GE = gross energy; DE = digestible energy; ME_m = ME requirement for maintenance calculated for individual cows; k_l = efficiency of ME use for lactation calculated for individual cows.

NS ($P > 0.05$); *** $P < 0.001$.

a1 to a4), or between HP and ME intake (equations b1 to b4), whereas different constants were obtained and compared within each group of different FP. Relating E_{l(0)} to ME intake produced a significantly higher constant in $P < 30\%$ group than in FP = 30 to 59%, and similarly in FP = 30 to 59% than in the 2 high FP groups ($P < 0.001$). The relationships between HP and ME intake generated a significantly lower constant in the FP <30% group than in the other 3 groups. Similar results were also found when comparing the coefficients, with a common constant, in the relationship between E_{l(0)} or HP and ME intake among the 4 groups (results not presented).

DISCUSSION

Effect of Dietary Forage Proportion on Energy Requirement for Maintenance

Being able to accurately determine energy requirements and energetic efficiencies is important to allow dairy cow rations to be properly formulated, irrespective of whether cows are being managed within either low or high input production regimens. The maintenance energy requirement is an important component of total energy requirements under various energy rationing systems, with maintenance energy being the energy

Table 3. Comparison of intercepts in linear relationships (with a common slope) between ME intake and energetic variables for lactating dairy cows offered diets containing different forage proportions^{1,2}

Forage proportion (%)	Equation	R ²	Equation no.
<30	E _{l(0)} = 0.631 _(0.0100) ME intake	0.88	a1
30–59			a2
60–99			a3
100			a4
30	HP = 0.355 _(0.0086) ME intake	0.67	b1
30–59			b2
60–99			b3
100			b4

^{a–c}Means with the same superscript letter are not significantly different ($P > 0.05$).

¹Unit = MJ/kg^{0.75} for E_{l(0)} (milk energy output adjusted to zero energy balance), HP (heat production), and ME intake.

²Values in parentheses are SE.

Figure 1. Linear relationships between ME intake and milk energy output adjusted to zero energy balance, for lactating dairy cows offered diets with different forage proportions (FP).

Figure 2. Linear relationships between ME intake and heat production for lactating dairy cows offered diets with different forage proportions (FP).

needed to maintain essential metabolic processes and tissue integrity. A major proportion of energy intake is used to support this process, and activity relating to eating, rumination, fermentation, and digestion (AFRC, 1993). Total energy expenditure for these activities is clearly related to the quantity and quality of feeds. Evidence indicates that maintenance metabolic rates are positively related to feed intake (Dong et al., 2015) and can be influenced by diet quality (Reynolds, 1996; Agnew and Yan, 2000).

However, current energy rationing systems, such as those used in the United Kingdom (AFRC, 1993; Agnew et al., 2004), United States (NRC, 2001), and France (Institut National de la Recherche Agronomique, INRA, 1989), give little consideration of the effect of diet quality on the maintenance energy requirement of dairy cows. In these systems (INRA, 1989; NRC, 2001; Feed into Milk, 2004), the maintenance energy requirement ($\text{MJ/kg}^{0.75}$) is assumed unchanged with a single fixed value for all dairy cows, irrespective of production levels and diet quality. The present study was designed specifically to examine the presence any effect of diet FP on maintenance energy requirement and k_1 by undertaking a meta-analysis of a large calorimeter chamber data set from lactating dairy cows of various milk production potentials, and offered forage-only diets or mixed diets containing low to high proportions of forage.

In the present study, the effect of dietary FP on maintenance energy requirement was evaluated using ANOVA and regression techniques. The results from both techniques demonstrated that dairy cows offered high forage diets (i.e., FP = 100% or 60–99%) had significantly higher ME_m or NE_M requirements ($\text{MJ/kg}^{0.75}$) than those given high-concentrate diets (e.g., FP <30%). For example, cows offered forage-only diets or mixed diets containing FP of 60 to 99% would require approximately 11% more energy for maintenance than those offered mixed diets containing FP of <30%. These results are in agreement with the findings of a previous study by Reynolds et al. (1991) in which cows receiving a 75% alfalfa diet had a higher HP than those offered a high-concentrate diet. An earlier study at this institute (Yan et al., 1997) reported that the maintenance energy requirement for lactating dairy cows was related to the forage/concentrate ratio of the diet, with ME_m values increased by 12 or 25% for diets containing 50 to 99% forage, and 100% forage (DM basis), respectively, when compared with low-forage diets (FP <50%). The higher ME_m values observed for cattle offered forage-based diets were suggested to be due to an increased energy expenditure associated with the digestive tract and other internal organs. Steen et

al. (1998) in a slaughter study with finishing lambs, showed that sheep offered diets containing a high proportion of silage had a significantly greater mass of alimentary tract than sheep offered diets containing a high proportion of concentrates. Webster (1981), in a review of scientific literature on the sources of energy expenditure, estimated that 45% of total HP was related to the gastrointestinal organs.

Effect of Dietary Forage Proportion on the Efficiency of ME Use for Lactation

The estimates of k_1 for individual dairy cows, determined as the ratio of $E_{l(0)}$ over ME available for production in the present study, were similar among the 4 FP groups. The k_1 values obtained in the present study (from 0.629 to 0.644) are relatively close to those reported by Yan et al. (2006; 0.647) and Dong et al. (2015) (0.641), but higher than those reported by Kebreab et al. (2003; 0.58) and Kirkland and Gordon (1999; 0.59). The mean k_1 value obtained in the present study (0.636 $\text{MJ/kg}^{0.75}$) is close to that of 0.638 calculated using equations recommended by AFRC (1993) and Standing Committee on Agriculture (SCA, 1990) ($k_1 = 0.35 \times \text{ME/GE} + 0.42$) and higher than that of 0.613 by Van Es (1978) and INRA (1989) ($k_1 = 0.24 \times \text{ME/GE} + 0.463$).

The effects of dietary composition on energy utilization efficiency have been extensively examined (Agnew and Yan, 2000). Some studies (Ørskov and Ryle, 1990) have examined the effects on the microbial population in the rumen, and consequently the production of VFA, when animals were offered diets with various forage proportions. It is well documented that high levels of dietary fiber contribute to VFA production with a high proportion of acetic acid, whereas the proportion of propionic acid increases as concentrate level increases in the ration (Flatt et al., 1969; McDonald et al., 1994). As milk fat concentration is linked to the molar proportion of acetic and butyric acids in rumen VFA, the VFA profile in the rumen is suggested to alter energy partitioning between milk and body tissue. For example, Huhtanen et al. (1993) reported that decreasing diet FP resulted in more energy being partitioned into body tissue and less into milk production. However, no evidence is available showing a significant relationship between k_1 and the molar proportion of acetic or propionic acid produced in the rumen (Agnew and Yan, 2000). The analysis of calorimeter chamber data by the regression technique in this study found little effect of diet FP on k_1 values of dairy cows. The effects of VFA on energy utilization have been studied by manipulation of dietary forage proportion or infusion of different levels of acetic

or propionic acid in the rumen. Sutton and Morant (1989) postulated that increasing concentrates in the diet would be expected to increase propionate production in the rumen such that glucose supply would be improved, thereby sparing AA for milk protein synthesis and providing more precursors for lactose synthesis. However, the infusion of different proportions of acetic and propionic acids into the rumen of lactating dairy cows showed no effect on k_i (Ørskov et al., 1969) or HP (Ørskov and MacLeod, 1982). Similar results were also observed by Tyrrell et al. (1979), namely that the infusion of acetic acid has little effect on HP of dry dairy cows offered forage-only diets. Yan et al. (1997) developed a set of linear relationships between $E_{l(0)}$ and ME intake to evaluate the effects of diet FP (<50% vs. 50–99% vs. 100%) on k_i values of lactating dairy cows, and found that the k_i derived from these relationships were very similar (0.62 to 0.64). Therefore, Agnew and Yan (2000) suggested that lower animal performance with dairy cows offered diets containing a higher FP might be due to a higher ME_m , leaving less energy available for production, rather than the high forage diet resulting in a lower k_i . The results of the present study support this hypothesis, namely that increasing forage proportions in the diet increases ME_m but has little effect on k_i values in lactating dairy cows.

CONCLUSIONS

The present meta-analysis of a large calorimeter data set from lactating dairy cows demonstrated that the maintenance energy requirement in lactating dairy cows was not a constant as recommended in many current energy feeding systems, but increases with increasing dietary forage proportion. However, diet forage proportion had no effect on the efficiency of ME use for lactation, a result similar to the reports published previously. The present result indicates that dairy cows managed under low-concentrate input or organic farming regimens may require more feed energy for maintenance than those reared in high-concentrate input systems. Using the current energy feeding systems to ration dairy cows managed under low-concentrate input systems may underestimate their nutrient requirement.

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APPENDIX

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