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Effects of stage of lactation on protein metabolism in dairy cows

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ABSTRACT

Forty-two lactating dairy cows were used to determine the interaction between folic acid and methionine dietary supplementation on protein metabolism at 6 and 25 weeks of lactation. Treatments were tested according to a 2 × 3 factorial arrangement, with two levels of methionine (0 vs 18 g of rumen protected methionine) and three levels of folic acid (0, 3, or 6 mg/d per kg of BW of pteroylmonoglutamic acid), equally distributed in 7 blocks of 6 cows each. Whole body leucine kinetics were determined using a constant infusion of L[1-^{13}C]leucine (1.8 mmol/h). Neither milk production, protein yield or leucine kinetics were affected by treatments. Milk production (45.5 to 35.4 ± 0.85 kg/d) and protein yield (1.43 vs 1.22 ± 0.028 kg/d) were higher (both $P<0.001$) at 6 vs 25 weeks of lactation. However, total whole body leucine irreversible loss rate was not affected by stage of lactation, but fractional oxidation increased as lactation advanced (0.136 vs 0.156 ± 0.0065; $P=0.03$). Whole body protein synthesis was not affected by the stage of lactation (4.14 and 4.08 ± 0.091 kg/d), but the partition of this synthesis was altered, with 0.453 vs 0.403 ± 0.0095 ($P<0.001$) of leucine used for protein synthesis directed towards milk output. However, absolute rates of non-milk protein synthesis were not affected by the stage of lactation. Although concentrations of IGF-1, insulin and somatotropin varied with stage of lactation, they did not correlate with protein metabolism. In the dairy cow, the high demand for milk production still represents an important portion of the leucine used for protein synthesis until mid-late lactation.

KEY WORDS: dairy cow, lactation, folic acid, rumen-protected methionine, leucine, kinetics

INTRODUCTION

Although it has long been assumed that biosynthesis by ruminal microflora of folic acid, vitamin B-9, was sufficient to cover the requirements of lactating dairy cows, recent work has shown that supplementary folic acid can increase milk and protein

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yields and/or milk protein concentration (Girard et al., 1995; Girard and Matte, 1998). As this was observed when estimated supply of methionine did not meet requirements of the lactating dairy cow, the mechanism proposed was that supplementary folic acid improved efficiency of transfer of one-carbon units to direct metabolism of homocysteine to anabolic methionine rather than loss to oxidation through the transsulphuration pathway (Girard and Matte, 2005).

In multiparous cows, the positive effect of folic acid was marked during early lactation but was lost by 200 d of lactation (Girard and Matte, 1998). This suggests an interaction between folic acid supplementation and stage of lactation related to a possible decreased demand for methionine as lactation progresses. First, in dairy cows, the demand for methionine to support protein synthesis likely decreases as lactation progresses: whole body irreversible loss rates (ILR) of amino acids (which include usage for both protein synthesis and oxidation) decreased with advancing lactation in goats (Riis, 1988; Bequette et al., 1994; Mabjeesh at al., 2000). In addition, the use of methionine as a methyl group precursor may also decline as lactation progresses. During early lactation, both demands for synthesis of glucose and for methylated compounds are increased. As these synthesis share common precursors, such as glycine and serine (Snoswell and Xue, 1987), this may create a shortage in precursors for synthesis *de novo* of methylated compounds. In such circumstances, part of the methionine supply may provide a direct source of methyl groups, reducing usage of methionine for protein synthesis. This metabolic pressure will lessen as lactation advances.

In growing ruminants, protein metabolism is closely linked to circulating concentrations of hormones such as insulin, IGF-1 and somatotropin (Lobley, 1992). Similarly, these hormones are known to vary with stage of lactation (Vicini et al., 1991) but the relationship between these hormones and protein synthesis in lactating dairy cows is not known.

Therefore, this study was undertaken to examine the interaction between dietary supplements of folic acid and methionine (supplied as a rumen-protected methionine supplement) at two stages of lactation on protein metabolism and to relate any difference to concentrations of hormones related to protein metabolism.

MATERIAL AND METHODS

Cows and treatments

Fifty-four multiparous Holstein cows from the dairy herd at the Agriculture and Agri-Food Canada Research Centre (Lennoxville, QC, Canada) were used to determine the effect of folic acid and methionine over a whole lactation. Cows

were assigned to 9 blocks of 6 cows each, according to their milk production during the previous lactation. During their lactation, all cows received, *ad libitum*, a total mixed ration containing, on a DM basis, %: grass silage 20.0, maize silage 20.1, high moisture maize 13.4, barley 18.9, wheat 6.0, soyabean hulls 2.0, soyabean meal 3.9, protected soyabean meal 3.9, blood meal 1.3, extruded soyabeans 3.8, Megalac® 1.14, tallow 0.43, urea 0.25, mineral and vitamin premix 4.9. The chemical composition of the ingredients are given in a companion paper (Girard et al., 2005). The total mixed ration was fed in eight equal meal per day offered every 3 h.

Methionine and folic acid supplementations were tested according to 2 × 3 factorial arrangement. Levels of methionine were 0 and 9 g/d of Smartamine M (Rhône-Poulenc Animal Nutrition, Mississauga, ON) before calving and 18 g/d of Smartamine M after calving. The basal diet was estimated to supply methionine as 1.75% of metabolizable protein (70% of estimated methionine requirement; NRC, 2001), while the diet plus Smartamine (analysed methionine content 88%, rumen by-pass 91% and digestibility 98%) was estimated to supply methionine at 2.2% of metabolizable protein. Folic acid levels (Rovimix 10% pteroylmonoglutamic acid, Hoffmann-LaRoche, Cambridge, ON, Canada) were 0, 3, or 6 mg/d per kg of BW of folic acid.

Cows were kept in a tie-stall barn under 16 h/d of light (05.30 to 21.30 h) and were milked twice daily at 12-h intervals. The experiment began 1 month before the expected time of calving and continued for a 305-d lactation period. Care of cows followed the recommended code of practice of Agriculture Canada (1990) and the guidelines of the Canadian Council of Animal Care (1993).

Sampling procedure

Seven of the nine blocks, i.e. forty-two cows, were used to determine the effect of treatments and stage of lactation on protein metabolism. At weeks 6 and 25 of lactation, leucine kinetics were determined using a 6-h primed (1.8 mmol) continuous infusion of L[1-^{13}C]leucine (1.8 mmol/h) into one jugular vein (from 09.00 to 15.00). From the contra-lateral jugular vein, three blood samples were collected before the start of the infusion to determine the natural abundance of ^{13}C in leucine and five hourly samples were collected starting two h after the beginning of the infusion (from 11.00 to 15.00 h). Simultaneous with the blood samples, breath was collected with a face mask, as previously described (Lapierre et al., 1999). In addition, seven hourly samples were collected from the jugular vein, from 09.00 to 15.00 h, to determine insulin and IGF-1 concentrations plus additional samples taken every 30 min for the determination of somatotropin concentrations. The CO_2 production was measured on the preceding day using a 6-h primed (0.4 mmol) continuous infusion (0.24 mmol/h) of [^{13}C]bicarbonate

(from 09.00 to 15.00 h), with three breath samples collected before the start of the infusion to determine the natural abundance of $^{13}CO_2$. Feed intake and milk production were recorded for six days preceding the infusions and milk was sampled at each milking.

Laboratory analyses

The isotopic enrichment (IE) of plasma free leucine was determined after deproteinization with sulphosalicylic acid and derivatization with N-(tert-butyldimethysilyl)-N-methyltrifluoroacetate-(MTBSTFA):acetronile (1:1), for m/z ions 302, 303 (Trio-1, VG Masslab, Manchester, UK), as described by Calder and Smith (1988). Purified breath CO_2 was analysed for [^{13}C] IE for m/z ions 44, 45, 46 on a triple collector isotopic ratio mass spectrometer (Sira 12, VG Masslab, Manchester, UK). Isotopic enrichments for leucine and CO_2 were corrected for background abundance and expressed as atom percent excess.

Total N in milk (protein = N × 6.38) was determined using a combustion procedure while total N in feed was analysed by micro-Kjeldahl method (AOAC, 1984). Double-antibody radioimmunoassays were used to determine concentrations of insulin, somatotropin and IGF-1 (Lapierre et al., 2000a,b). Intra-assay and inter-assay coefficients of variation were, respectively, 5.1 and 4.8% for insulin, 1.6 and 1.6% for somatotropin, 5.0 and 5.4% for IGF-1.

Calculation and statistical analyses

For all given equations, the rate of infusion is mmol/h and the IE of the infusate, leucine or CO_2 is atom percent excess. Whole body leucine ILR (irreversible loss rate; mmol/h) was calculated as:

$$((\text{rate of leucine infusion} \times IE_{infusate}) / IE_{leu}) - (\text{rate of leucine} \times IE_{infusate})$$

where IE_{leu} represents the IE of the precursor pool, taken as plasma free leucine, calculated as the arithmetic mean of samples taken between 2 to 6 h of infusion, under plateau conditions.

Whole body leucine oxidation (mmol/h) was calculated as:

$$(IE_{\text{expired CO2}} \times CO_2 \text{ production (mmol/h)} / IE_{leu}) - (\text{rate of leucine infusion} \times IE_{infusate})$$

where the IE of CO_2 was measured the day of leucine infusion.

Whole body fractional rate of leucine oxidation (FO) was calculated as:

$$\text{leucine oxidation} / \text{ILR}$$

The CO_2 production (mmol/h) was estimated by bicarbonate infusion and calculated as:

$$(\text{rate of bicarbonate infusion} \times IE_{infusate} / IE_{\text{expired CO2}}) - (\text{rate of infusion} \times IE_{infusate})$$

where the IE of CO_2 was measured the day of bicarbonate infusion.

Leucine used for whole body protein synthesis was calculated as the difference between whole body leucine ILR and leucine oxidation. Protein synthesis was then estimated assuming constant fractions of 63 g of leucine/kg of synthesized tissue protein (Lobley et al., 1980) and 98 g of leucine/kg of milk protein (Swaisgood, 1995). Protein synthesis related to milk synthesis was estimated using milk protein output.

Statistical analyses

Two cows were removed from statistical analyses, due to health problems not related to the experimental treatments that occurred at calving or in early lactation. Data were analysed using the MIXED procedure of SAS (1999) according to a randomized complete block design with repeated measures in time. The treatment structure was a complete factorial arrangement with two levels of methionine and three levels of folic acid. Results are reported as least squares means and SEM.

RESULTS

Treatments had no effect ($P>0.20$) on any of the leucine kinetics parameters measured. The only effect of treatment was an increase (32.2 to 33.9±0.38 g/kg; $P=0.004$) in crude protein concentration in milk with the addition of rumen protected methionine. However, there was no effect of rumen protected methionine ($P=0.86$) on protein yield which averaged 1.33 and 1.32±0.033 kg/d, for the 0 vs the 18 g/d of rumen protected methionine.

As expected, milk production decreased ($P<0.001$) from 45.5 to 35.4±0.85 kg/d between wk 6 and 25 of lactation. Over the same period, protein concentration increased (31.4 vs 34.6±0.35 g/kg; $P<0.001$) while total protein yield decreased (1.43 vs 1.22±0.028 kg/d; $P<0.001$). Neither dry matter nor nitrogen intake were affected by stage of lactation and averaged 25.4 vs 25.0±0.41 kg/d and 670 vs 671±11.2 g/d, respectively.

Leucine kinetics are presented in Table 1. The stage of lactation had no effect on whole body leucine ILR, leucine oxidation or total leucine used for protein synthesis. However, the relative partition of ILR was altered by the stage of lactation. Cows at 6 weeks of lactation had a lower fractional oxidation rate of leucine than cows at 25 weeks of lactation (0.136 vs 0.156±0.0065; $P=0.03$). Whole body protein synthesis decreased numerically in later lactation but with a larger decline for leucine secreted in milk protein ($P<0.001$). In consequence, non-milk protein synthesis remained unaltered. Therefore, for cows in early lactation, an increased proportion of their total protein synthesis was towards milk output (0.453 vs 0.403±0.0095; $P<0.001$) with a corresponding reduced proportion as non-milk protein synthesis (0.547

TABLE 1

Effect of stage of lactation on leucine kinetics in dairy cows[1]

Leucine kinetics, mmol/h	Stage of lactation, weeks		SEM	P
	6	25		
Whole body ILR[2]	114.5	112.9	2.49	0.58
Oxidation	15.9	17.7	0.95	0.13
Fractional oxidation	0.136	0.156	0.007	0.03
Used for protein synthesis	98.6	95.2	1.96	0.16
milk protein output	44.3	38	0.86	<0.001
non-milk protein synthesis	54.3	57.2	1.69	0.16

[1] least squares means with pooled SEM
[2] ILR: irreversible loss rate

vs 0.597±0.0095; P<0.001) compared with later lactation. The total amount of protein synthesized averaged 4.14 and 4.08±0.091 kg/d, with 1.43 and 1.22 kg excreted as milk protein at 6 or 25 weeks of lactation, respectively.

TABLE 2

Effect of stage of lactation on hormone concentrations[1]

Hormone	Stage of lactation, weeks		SEM	P
	6	25		
IGF-1, ng/mL	122.5	151.2	5.33	<0.001
Insulin, ng/mL	0.57	0.83	0.034	<0.001
Somatotropin, ng/mL	5.4	2.8	0.31	<0.001

[1] least squares means with pooled SEM

Insulin and IGF-1 increased (P<0.001) with stage of lactation while somatotropin decreased (P<0.001; Table 2). There was no significant correlation between these hormones and ILR or total protein synthesis (r^2<0.20 with P>0.10).

DISCUSSION

The absence of treatment effects on protein yield and the impact of methionine on milk protein concentration is consistent with observations made on the whole lactation and has been discussed in the companion paper (Girard et al., 2005). Briefly, the absence of a folic acid effect could be due to the low serum concentrations of vitamin B_{12} measured in these cows, which would restrict methionine synthase activity and lead to 'trapping' of folates as methyltetrahydrofolate. The lack of effect of methionine supplementation may be due to the high dry matter intakes that may override the estimated deficiency of methionine, calculated relative to total protein

supply and not as a net supply per day. In consequence the major responses in this study relate to the effect of stage of lactation on protein metabolism.

Whole-body leucine ILR in these animals is similar to values previously reported in dairy cows, using plasma leucine as representative of the precursor pool (86 to 121 mmol/h: Bequette et al., 1996; Lapierre et al., 2002; Thivierge et al., 2002). In parallel with observations on milk protein yield, treatments did not affect protein metabolism. This is the first study, however, to consider how stage of lactation might impact on whole body protein kinetics in dairy cows and where very little effect on ILR was observed. This contrasts with reports in dairy goats, where animals in mid to late lactation had a lower whole body ILR based on either leucine (by 35%: Riis, 1988; 22%: Bequette et al., 1994), phenylalanine (by 16%: Bequette et al., 1994) or lysine (by 38%: Mabjeesh et al., 2000) compared with goats in early lactation. Such differences highlight the caution needed when extrapolations are made between ruminant species but raise the intriguing question - why are there differences between lactating caprines and bovines? Several possibilities exist with foremost, perhaps, the observation that in the current study neither dry matter nor N intake decreased during lactation, while in the dairy goat studies, intake was reduced in later lactation. Thus, nutrient supply (including leucine) was maintained throughout lactation in the dairy cows but declined in the goats with a consequent lowering of ILR. Furthermore, ILR is a composite of leucine used for protein synthesis and leucine oxidation, but the latter was not determined in the dairy goat studies. Therefore, it is unknown what component(s) of ILR decreased with advancing lactation in the caprine. In the dairy cows, the lack of change in whole body ILR masked an increase in oxidation, particularly when expressed in fractional terms.

Another explanation for the difference between dairy goats and cows might involve the relative importance of milk production and the temporal changes during the lactation cycle between the species. In the dairy goats, milk production represented a lower proportion of ILR and changes over time were more dramatic, with milk production approximately halved between early and late lactation. In contrast, milk protein output in the current dairy cows decreased by only 14%. Thus, for the dairy cows the proportion of ILR used for milk protein secretion showed a modest decrease during lactation from 0.39 to 0.34±0.007, while in the dairy goats studies, the proportion declined from 0.30 to 0.19 (Bequette et al., 1994) or remained unaltered at a much lower proportion (approximately 0.15; Riis, 1988; Mabjeesh et al., 2000).

In agreement with observations in goats by Bequette et al. (1994), the non-milk ILR was not affected by the stage of lactation in the dairy cow. Indeed, the amount of leucine used for non-milk protein synthesis throughout lactation, averaging 55.8 mmol/h, is similar to that observed for cows in later lactation (averaged 55.7 mmol/h at 210 days in milk) and producing only 16.8 kg/d of milk (Lapierre

et al., 2002). Overall, the efficiencies in excess of 30% for conversion of whole body protein synthesis to a commercial protein product ensure that the dairy is an efficient ruminant compared to the beef animal, where the ratio of protein retention on synthesized protein is closer to 10% (Hammond et al., 1987; Lapierre et al., 1999).

Variations of hormones across stage of lactations were as expected based on other literature reports, i.e. a decrease in somatotropin and an increase in IGF-1 and insulin (Vicini et al., 1991). In growing ruminants, relationships between protein synthesis (or degradation) and these hormones have been postulated (Lobley, 1992), but no evidence of similar correlations were found for the current lactating animals. In growing ruminants, IGF-1 concentrations, closely linked with the nutritional status of the animal, match well with anabolic performance. In dairy cows, IGF-1 concentrations, still linked with the nutritional status of the animal, are low during early lactation (Vicini et al., 1991) as the animals are in low or negative balance. However, this period corresponds to the most productive period for the dairy cow and therefore, no correlation can be found between whole body protein synthesis and circulating concentrations of IGF-1. Biological activity of IGF-1 is not only related to circulating concentrations but also to its binding proteins which are related to nutritional status (Lapierre et al., 1995) and probably the stage of lactation. Furthermore, seeking relationships between circulating hormone concentrations and protein anabolism in dairy cows also ignores critical changes in tissue sensitivity to these hormones through lactation, as has been observed for insulin (Vicini et al., 1991). Therefore, a direct link between hormone concentrations and protein synthesis could not be observed in lactating animals across lactation.

In conclusion, whole body ILR of leucine in dairy cow is not altered between early to mid-late lactation, where milk production still represents an important fraction of whole body protein synthesis. Protein synthesis required for other functions than milk output was also not affected by the stage of lactation. Altogether these data reinforce the large contribution that milk protein secretions make to whole body protein synthesis in the high producing dairy cow, making the cow one of the most efficient ruminants for transformation of ingested plant protein into high quality animal protein for human consumption.

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STRESZCZENIE

Wpływ okresu laktacji na przemianę azotu u krów mlecznych

Doświadczenie przeprowadzono na 42 krowach mlecznych celem oznaczenia współzależności pomiędzy dodatkiem kwasu foliowego i metioniny do dawek na przemianę azotu w 6 i 25 tygodniu laktacji. Zastosowano układ czynnikowy 2 × 3, z dwoma poziomami metioniny (0 vs 18 g chronionej metioniny) i trzema poziomami kwasu foliowego (0, 3 i 6 mg/dzień/kg m.c.) w postaci kwasu pteroilomonotaminowego, jednakowo podzielonych do 7 bloków, po 6 krów każdy. Kinetykę leucyny w całym ciele oznaczano przy stałej infuzji ($1^{-13}C$) leucyny (1,8 mmol/godz.). Zastosowane dodatki nie wpłynęły na produkcję mleka i białka oraz kinetykę leucyny. Produkcja mleka (45,5 do 35,4±0,85 kg/d) oraz białka (1,43 vs 1,22 ± 0,028 k/d) były większe (w obydwóch przypadkach $P<0,001$) w 6 niż w 25 tygodniu laktacji. Jednakże tempo nieodwracalnych strat leucyny w całym ciele nie zależało od okresu laktacji, lecz stopień utleniania zwiększał się wraz z postępującą laktacją (0,136 vs 0,156 ± 0,0065; $P=0,03$). Okres laktacji nie miał wpływu na syntezę białka w ciele (4,14 i 4,08 ± 0,91 k/d), lecz względna wartość tej syntezy była zróżnicowana, 0,453 vs 0,403 ± 0,0095 ($P<0,001$) leucyny wykorzystanej do syntezy białka bezpośrednio wydzielanego w mleku. Bezwzględne tempo (g/d) syntezy białka nie będącego składnikiem mleka było niezależne od okresu laktacji. Chociaż stężenie IGF-1, insuliny i somatotropiny zmieniało się wraz z przebiegiem laktacji, to jednak nie było dobrze skorelowane z przemianą białka. U krów mlecznych, o wysokim zapotrzebowaniu na produkcję mleka, istotna część leucyny używana jest do syntezy białka w środkowym okresie laktacji.