Small Ruminant Research 112 (2013) 162–173

Contents lists available at SciVerse ScienceDirect

Small Ruminant Research

journal homepage: www.elsevier.com/locate/smallrumres

Intravenous supplementation of acetate, glucose or essential amino acids to an energy and protein deficient diet in lactating dairy goats: Effects on milk production and mammary nutrient extraction

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ARTICLE INFO

Article history:
Received 14 February 2012
Received in revised form
30 November 2012
Accepted 1 December 2012
Available online 5 January 2013

Keywords:
Mammary metabolism
Mammary nutrient uptake
Arterio-venous concentration difference
Acid–base parameters

ABSTRACT

In the present experiment we aimed to study, if milk synthesis is more sensitive toward deficiency in supply of amino acids in early (EL) versus late lactation (LL), and if energy yielding substrates in the form of acetate (but not glucose) can contribute to sustain milk (protein) synthesis, when amino acid supply is suboptimal. Goats were fed a basal diet deficient in energy (90% of requirements) and protein (80% of requirements), and were randomly allocated to 4 treatments in a balanced 4×4 Latin square design. The treatments consisted of 4-d continuous intravenous infusions of isoosmotic, isoenergetic solutions of essential amino acids (EAA), sodium acetate (ACE) and glucose (GLU) with saline (SAL) as control. There was a 3-d rest period between treatments. Milk production was recorded during the last 48 h of the infusion. Arterio-venous concentration differences (AVD) across each udder half (gland) were determined every 4 h during the last 24 h of infusion for blood acid–base parameters and key plasma metabolites.

In EL, and compared to the SAL treatment, gross milk yield was increased significantly by GLU and with a tendency by EAA, ECM yield by ACE treatment, milk protein yield by EAA and close to significantly by ACE, but not by GLU treatment. GLU reduced milk protein percentage compared to all other treatments. High milk protein yields on EAA and ACE treatments were associated with higher arterial AVD for acetate and oxygen (not significant for ACE), and higher AVD also for β-hydroxybutyrate on EAA treatment compared to GLU and SAL.

In LL, EAA increased ECM compared to all other treatments, increased milk protein yield and percentage compared to GLU and protein yield close to significantly compared to ACE. Fat percentage and milk fat yield were also significantly or numerically lower on GLU compared to all other treatments in LL, and this was associated with lower AVD across the mammary gland for glucose, β-hydroxybutyrate and long chain fatty acids.

In conclusion, the mammary gland is sensitive toward insufficient EAA supply in both EL and LL. Interestingly, increased mammary supply of ACE, but not GLU, could compensate for insufficient EAA supply in EL, but this was not the case in LL. This suggests that acetate (or β-hydroxybutyrate) can improve mammary amino acid utilization for protein synthesis in EL by generation of ATP from oxidation, potentially pointing to a scope for differential protein–energy recommendations for ruminants across the lactation period.

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http://dx.doi.org/10.1016/j.smallrumres.2012.12.001

1. Introduction

Consumers' increased demand for protein has promoted the value of milk protein production over the last decades. Milk protein synthesis in dairy cows has been shown to be stimulated by increased amino acid supply either through dietary protein supplementation (Hanigan et al., 2001; Rulquin et al., 1993; Weekes et al., 2006) or by intravascular infusion of amino acids (Kim et al., 2000; Metcalf et al., 1996). However, increased mammary supply of a number of specific amino acids did not always have a positive impact on milk protein production (Seymour et al., 1990). Synthesis of protein in the mammary gland as well as in other body tissues relies not only on building blocks in form of amino acids, but also on availability of energy in the form of ATP. Raggio et al. (2006) therefore suggested that milk protein production could be improved by protein as well as energy supply to the mammary gland. Thus, intravascular infusion of energy yielding substrates like acetate (Chaiyabutr et al., 1998; Maas et al., 1995; Weekes et al., 2006) and glucose (Bobe et al., 2009; Schei et al., 2007) has been shown to affect milk protein synthesis positively.

Acetate and glucose are the major energy suppliers to the mammary gland. Acetate is utilized in oxidative phosphorylation of adenosine nucleosides, which results in the generation of ATP (Forsberg et al., 1984; Scott et al., 1976), whereas glucose is oxidized mainly through the pentose phosphate pathway to yield NADPH required for *de novo* fatty acid synthesis (lipogenesis) (Chaiyabutr et al., 1980, 2008). If mammary energy supply is a main determinant for protein synthesis; it should theoretically be possible to substitute amino acids to some extent in the diet with an energy yielding substrate to provide extra ATP in the mammary gland and improve utilization of the amino acids available.

With progressing lactation, the milk production efficiency decline and the milk composition in dairy animals change as a result of declined number and activity of the secretory cells in the mammary tissue (Safayi et al., 2010; Safayi and Nielsen, 2009; Wilde and Knight, 1989). Along with these changes, mammary nutritional requirements and uptake are also changed (Aganga et al., 2002; Nielsen et al., 2001). There are indications suggesting that this is associated with an altered sensitivity of the mammary gland toward variations in e.g. amino acid supply, since correlations between arterial concentrations and arteriovenous differences (efficiency of mammary uptake) for individual amino acids differed in early compared to late lactation in dairy goats fed different levels of lysine and methionine (Madsen et al., 2005). Therefore, it is also likely that there might be a prospect for differentiating protein recommendations for ruminants across the lactation period, and still maintain protein production by optimization of the provision of energy yielding substrates relative to amino acids (Madsen et al., 2005).

We hypothesized that milk synthesis is more sensitive toward deficiency in supply of AA in early (EL) compared to late lactation (LL), and that energy yielding substrates contributing to generation of ATP in the mammary gland can contribute to sustain milk (protein) synthesis, when amino acid supply is suboptimal. The more specific aims of the present project were to determine whether: (1) provision of energy (ATP) yielding substrates can compensate for an insufficient AA supply to the mammary gland and hence improve overall utilization of AA for milk protein synthesis, (2) acetate is more efficient than glucose in stimulating milk synthesis and particularly its milk protein content due to their believed contribution to mainly ATP and NADPH, respectively, and (3) milk synthesis is more sensitive toward such changes in nutrient provision in EL compared with LL. This issue is of major importance for the economy of dairy production by increasing our knowledge on how to maximize not only the milk protein yield but also the overall nitrogen utilization in dairy farming.

The objectives were addressed in a study with goats conducted in both early and late lactation. The goats were fed a basal ration designed to meet approximately 90% and 80% of daily requirements for net energy and amino acids absorbable from the small intestine, respectively, and given intravenous infusions of isoosmotic solutions of essential amino acids (EAA), acetate (ACE), glucose (GLU) and saline (SAL) as control in a 4×4 Latin square design.

2. Materials and methods

2.1. Experimental design

The experiment was carried out at the experimental facilities at the Faculty of Life Sciences, University of Copenhagen, Denmark, and approved by the Danish Animal Experimentation Inspectorate, and complied with the Danish Ministry of Justice laws concerning animal experimentation and care for experimental animals (www.retsinformation.dk/forms/r0710.aspx?id=2862).

Four Danish Landrace dairy goats (parity ≥ 2) were used in this experiment. Goats were previously surgically prepared with exteriorized carotid arteries and milk veins, as described by Nielsen et al. (1995). The goats were randomly assigned to one of four treatments in a balanced 4×4 Latin square design, which was performed in both late lactation (LL) and the following early lactation (EL). Due to health reasons, one of the goats had to be replaced in the early lactation trial with her twin sister, which had a similar size, body weight and milk yield. At the start of each part of the experiment, early and late lactation, the goats were 21 ± 1 and 157 ± 9 days postpartum, and live weights were 51 ± 8 and 52 ± 3 kg, respectively.

Treatments consisted of continuous intravenous infusions of 4 isoosmotic solutions at pH 7.4 (dietary provision of 960 g/d for 4 days) containing either saline (SAL) as control, a mixture of essential amino acids (EAA) composed to match the relative proportion of EAA in milk protein determined in a previous experiment with this goat breed (Madsen et al., 2005), sodium acetate (ACE), or glucose (GLU). Energetic value of individual nutrients were calculated from the maximal possible yield of ATP upon complete oxidation of that nutrient in biochemical pathways, with correction for ATP expenses associated with synthesis of urea following amino acid oxidation, and setting the energy captured in ATP to 52 kJ/mol (equivalent to ΔG in hydrolysis of ATP to ADP under the physiological conditions prevailing in the mammalian cell) (Boisen, 1998). The chemical composition of the feed used in both early and late lactation as well as an overview of the daily provision of energy and protein to the goats with the daily diet and infusion solutions are shown in Tables 1 and 2. EAA, ACE and GLU infusions were composed to be isoenergetic based on the potential yield of ATP from oxidation of these nutrients in the body (33.6, 10 and 36 mol ATP/mol EAA mix, ACE and GLU, respectively). Calculated theoretical ATP yields from oxidation of individual amino acids were reported previously by Boisen (1998), and ATP yields of acetate and glucose were calculated based on general biochemical pathways (Berg et al., 2002). Infusion solutions were made weekly. Each treatment period lasted one week, where the intravenous infusions were initiated at 12:00 on day 0 (Monday) and concluded at 12:00 on day 4 (Friday), followed by a 3-day rest period in between. Total energy intake and calculated amounts of amino acids absorbed from the small intestine (sum of dietary derived amino acids estimated by the Danish protein evaluation system included