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Invited review: Current representation and future trends of predicting amino acid utilization in the lactating dairy cow

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ABSTRACT

In current dairy production systems, an average of 25% of dietary N is captured in milk, with the remainder being excreted in urine and feces. About 60% of total N losses occur postabsorption. Splanchnic tissues extract a fixed proportion of total inflow of each essential AA (EAA). Those EAA removed by splanchnic tissues and not incorporated into protein are subjected to catabolism, with the resulting N converted to urea. Splanchnic affinity varies among individual EAA, from several fold lower than mammary glands' affinity for the branched-chain AA to similar or higher affinity for Phe, Met, His, and Arg. On average, 85% of absorbed EAA appear in peripheral circulation, indicating that first-pass removal is not the main source of loss. Essential AA in excess of the needs of the mammary glands return to general circulation. High splanchnic blood flow dictates that a large proportion of EAA that return to general circulation flow through splanchnic tissues. In association with this constant recycling, EAA are removed and catabolized by splanchnic tissues. This results in splanchnic catabolism equaling or surpassing the use of many EAA for milk protein synthesis. Recent studies have demonstrated that EAA, energy substrates, and hormones activate signaling pathways that in turn regulate local blood flow, tissue extraction of EAA, and rates of milk protein synthesis. These recent findings would allow manipulation of dairy diets to maximize mammary uptake of EAA and reduce catabolism by splanchnic tissues. Dairy cattle nutrient requirement systems consider EAA requirements in aggregate as metabolizable protein (MP) and assume a fixed efficiency of MP use for milk protein. Lysine and Met sufficiency is only considered after MP requirements have been met. By doing so, requirement systems limit the scope of diet manipulation to achieve improved gross N efficiency. Therefore, this review focuses on understanding the dynamics of EAA metabolism in

mammary and splanchnic tissues that would lead to improved requirement prediction systems. Inclusion of variable individual EAA efficiencies derived from splanchnic and mammary responses to nutrient and hormonal signals should help reduce dietary protein levels. Supplementing reduced crude protein diets with individual EAA should increase gross N efficiency to more than 30%, reducing N excretion by the US dairy industry by 92,000 t annually.

Key words: nitrogen utilization, essential amino acid requirement, mammary gland, splanchnic tissue

INTRODUCTION

Agriculture in general and the dairy industry in particular are under increasing pressure from federal and local governments and from consumers to reduce their environmental footprint. Among the dairy industry pollutants, N excretion is a major concern because of its impact on air and water quality, ecosystem biodiversity, and human health. Nitrogen export to the environment can result in eutrophication of aquatic ecosystems and coastal hypoxia; increased atmospheric particles, decreased stratospheric ozone concentrations, and greenhouse gas concentrations; increased acidity of precipitation, soil, and surface water; aggravation of asthma in people; and denigration of drinking water contributing to methemoglobinemia in infants (Wolfe and Patz, 2002). In addition to the environmental impact of nitrogen, protein—the source of the waste N—is an expensive dietary nutrient, representing approximately 42% of the cost of lactating cow rations (St-Pierre, 2012). Improving gross N efficiency would improve dairy economics, reduce environmental impact, and reduce demand for animal feed protein sources.

There are approximately 9 million dairy cattle in the United States (USDA-ERS, 2012). In a survey carried out on 103 large dairies across the country (613 ± 46 cows and 34.5 ± 0.3 kg of milk sold per cow per day), nutritionists reported feeding diets that averaged $17.8 \pm 0.1\%$ CP (Caraviello et al., 2006). A meta-analysis using 846 experimental diets with similar average CP content reported a mean gross N efficiency of $24.7 \pm$

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3.99% (Hristov et al., 2004b). Thus, over a 10-mo lactation, assuming the same dietary conditions (22.1 kg/d DMI and 17.8% CP) reported by Hristov et al. (2004b), 1.3 million tonnes of dietary N would have been excreted in the United States.

To reduce the environmental impact of the dairy industry, it is necessary to know the potential maximal gross N efficiency for milk protein production, where N is lost, and what approaches can be used to mitigate those losses and improve gross N efficiency. Dietary N that is not incorporated into milk is mostly excreted in feces or urine. Fecal N includes undigested dietary, microbial, and endogenous N. The latter represents between 18 and 31% of fecal N and includes undigested proteins secreted along the gut, sloughed cells from the gut mucosa, and urea recycled to the hindgut (Lapierre et al., 2008; Røjen et al., 2012), which are not particularly responsive to varying dietary N levels. Similarly, intestinal digestibility of bacterial protein and RUP from individual ingredients is considered fixed by nutrient requirement systems (NRC, 2001).

Unlike fecal N, urinary N excretion is highly responsive to varying N intake (Lobley et al., 2000a; Lapierre and Lobley, 2001; Reynolds and Kristensen, 2008). When dietary N is not highly restricted, most of the urinary N is excreted as urea produced in the liver from 2 sources: ruminal ammonia and postabsorptive AA catabolism (Lobley et al., 2000b; Marini and Van Amburgh, 2003). At low levels of N supply, other sources of N such as ammonia can represent a significant proportion of total N excreted in urine and can even surpass the amount of N excreted as urea (Wickersham et al., 2008, 2009). The relative contribution of rumen ammonia and postabsorptive AA catabolism to the total amount of urea produced in the liver depends on how well the N supply matches ruminal and postabsorptive requirements. When RDP was supplemented in excess of the microbial utilization capacity, ammonia absorption from the rumen and N excretion in urine increased (Hristov et al., 2004a). Thus, excess RDP reduces gross N efficiency, but the efficiency of MP for milk protein synthesis (MPLE) does not change (Cyriac et al., 2008). On the other hand, increasing RUP supply increases duodenal absorption of both EAA and NEAA, and when the absorbable supply of AA exceeds MP requirements for maintenance, lactation, gestation, and growth, excess AA are catabolized, increasing N excretion in urine. Therefore, by matching MP supply with maintenance and production requirements, MPLE should be maximized, and urea production and urinary N excretion should be minimized. However, even when MP just meets requirements, some EAA are likely limiting, whereas other EAA are provided in excess of their

individual requirements and are subject to catabolism. This latter group represents an inefficiency.

Swine and poultry nutritionists formulate rations with reduced protein levels and supplement with specific EAA to minimize overfeeding of most EAA. Using this approach results in gross N efficiencies of 40% or greater (Nahm, 2002). Baker (1996) made maximal use of this strategy and demonstrated that postabsorptive N efficiency in pigs can reach 85% when the supply of each EAA matches tissue needs. That efficiency is in agreement with the maximal theoretical efficiency of the mammary glands (MG) to convert an ideal absorbed EAA profile into milk protein, as considered by the UK Nutrient Requirement System for Ruminants (AFRC, 1992). Dijkstra et al. (2013) discussed potential losses that explain why maximal theoretical partial efficiencies cannot be achieved at the animal level. The inevitable losses included endogenous N losses in urine and feces, microbial nucleic acids, undigested AA, and catabolism of absorbed AA (Dijkstra et al., 2013). However, reducing dietary CP to 15% or lower and supplementing with individual EAA should increase gross N efficiency to 30% or greater (NRC, 2001; Haque et al., 2012) and reduce N losses by 92,000 t/yr in the United States. If such a reduction in dietary protein could be achieved industry-wide with no loss in production, the reduction in need for high-protein meal ingredients translates to 543,000 fewer hectares of land used to grow soybeans, assuming a yield of 2,700 kg/ha (NASS, 2013). Feeding such low levels of dietary protein requires very accurate and precise predictions of nutrient requirements to avoid potential losses in milk production and dairy income. Therefore, the focus of this review is on experimental and modeling work investigating MG and splanchnic metabolism of EAA, as well as their effect on cell signaling regulation of milk protein synthesis. The objective is to delineate modeling approaches that will address the current deficiencies and lead to model systems that can be used to increase postabsorptive MPLE.

CURRENT REPRESENTATION OF EAA SUPPLY AND REQUIREMENTS

The National Research Council (NRC, 1989, 2001) equations, especially the postabsorption protein system, are used in whole or in part by most ration balancing software packages in the United States. Thus, components of the protein system encoded in the Dairy NRC (1989, 2001) models (the latter being referred to as NRC-2001 for the remainder of this work) are used to determine protein supplementation in most US dairy diets. The NRC-2001 predicts flow of MP and digest-

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