TERMINATION REPORT

Project Number: NC-1040
Project Title: Metabolic Relationships in Supply of Nutrients for Lactating Cows.
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ACCOMPLISHMENTS:

Research efforts addressed nutritional and metabolic issues associated with milk production in the high yielding dairy cow. These efforts were justified by the continuously changing environment of the US dairy industry ranging from the economic need to use/availability of novel feed by-products, new discovery in metabolism impacting the way animals throughout critical periods, such as the transition from late pregnancy to early lactation, availability of tools to better understand genetic mechanisms underlying efficiency and continued need to improved feeding systems. The major accomplishments will be described under each of 3 specific objectives of the project.

Specific objective 1: to quantify properties of feeds that determines the availability and utilization of nutrients critical to milk production.

This specific objective addressed the need to find the optimal combination of chemical and physical properties of feeds that provides the proper amount and balance of absorbed nutrients. This is a challenge because of the tremendous variety and physical properties (either inherent or altered by various processing methods) of feedstuffs, the complexity of interactions among feed particles, nutrients and organisms in the rumen, and their interactions with intestinal digestion.

Three teams focused their work on the rumen. The OH team documented the responses of ruminal protozoa to various compounds used to assess signal transduction in eukaryotic cells. These results explain the migratory ecology of fully ciliated isotrichid protozoa: they go from the ventral to the dorsal rumen to consume sugars to perform glycogenesis, followed by active swimming back to the ventral rumen. This work suggested that isotrichids spill energy through glycogen cycling. Thus, increasing numbers of these protozoa might explain lower than predicted efficiency of microbial protein synthesis in the rumen. In contrast, the entodiniomorphids have cilia only near their oral region. Motility is integrated with phagocytosis to support their ability to synchronize cell growth rate with particulate passage rate. Ruminal protozoa are the main contributors to excess proteolysis in the rumen and also produce hydrogen that fuels methanogenesis. The MN team focused on rumen microbes and assessed the impact of various factors (monensin, dietary sulfur, yeast addition, etc.) on microbial metabolism and how they influence availability of nutrients to the small intestine. Moreover, this team also conducted a number of studies to compare various techniques for estimating intestinal protein digestion (e.g., immobilized digestive enzyme assay *vs* cecectomized rooster bioassay). The IA team found that feeding a commercial probiotic (lactate-producing and lactate-using microorganisms) to lactating dairy cows results in a significant (about 8%) improvement in feed efficiency for milk production.

Fiber is the largest single nutritional component of forage crops. Lack of fiber leads to increased prevalence of digestive disorders and associated negative effects on performance (inconsistent intake and reduced digestibility of feed, reduced microbial protein synthesis, etc,). Finding how much digestible fiber can be included in the diet without negatively impacting milk production remains an important issue. Work in KS helped to define metrics for meeting the fiber requirements of lactating cows without limiting milk production by constraining energy intake. Researchers at UT identified optimal feeding program and management that improved utilization of forages to typical lactation dairy diets. They focused on selection of corn silage hybrids to maximize ruminal fermentation, nutrient utilization, and productive performance of dairy cows. In addition, they investigated dietary approaches to improve nutritive value of alfalfa hay with emphasis on its nitrogen utilization efficiency. All of these efforts took into account the need to formulate cost-effective diets. The OH team optimized the efficiency of usage of forage and non-forage fiber relative to starch and sugar concentration for dairy diets. They compared various forages when corn milling co-product increased from 20 to 30% in low starch diets: they found that grass hay offered benefits by increasing rumination whereas alfalfa hay improved feed efficiency when effective fiber was adequate.

A wide variety of by-products processing methods are available but safe levels of inclusion and overall effects on milk yield were not well defined. The SD research team evaluated different inclusion rates of distiller grains in dairy cow rations and showed that up the inclusion can reach 30% of the ration dry matter with no detrimental effects. They also showed that distiller grains could be used with all type of forages (corn silage, alfalfa haylage, alfalfa hay, and corn stalks and the by-product soy hulls). Moreover, they demonstrated that starch levels in the diet could be reduced when feeding distiller grains or other distiller grains by-products. This had the dual advantage of reducing feed costs and improving feed efficiency. Another group in ND evaluated the effects of dietary supplementation of various oil seeds on the yield and composition of milk and the extent to which fatty acids were altered during rumen bio-hydrogenation. They found that flaxseed (and other oils seeds) could supplement protein and energy needs during lactation and at the same time increased milk content of omega-3 fatty acids. In the case of flaxseed, minimal processing was needed to achieve these effects. The IN team examined the use of biofuel co-products including distillers grains and soy diesel glycerol on milk production, milk composition and feed intake. Results indicate that prestorage blending of distiller's grains with either corn or haycrop silage extends the feeding time for wet distiller's grains and is without effect on milk productions or composition. Other experiments indicate that glycerol can replace corn grain in diets for transition and lactating cows and supports equivalent levels of milk. Glycerol reduced feed sorting in transition cow diets and slightly improved animal health and productivity.

PA researchers showed that essential oils and herbs could decrease enteric methane production as well as improve feed conversion as long as dry matter intake is not negatively affected. Medium-chain fatty acids had a strong anti-protozoal effect in the rumen and could modify the milk fatty acid profile but also decrease feed intake. In a series of laboratory and greenhouse experiments, they demonstrated that manure from dairy cows fed protein-deficient diets had substantially lower ammonia emissions and decreased nitrate losses. Urinary urea was the primary source of ammonium in manure contributing over 80% of the ammonia-nitrogen losses in the first 10 days of storage.

Evidence that early life nutrition impacts future milk production is accumulating. The Provimi group in OH investigated nutrient requirements of neonatal calves. They demonstrated that calves respond to supplementing amino acids and fatty acids through milk or starter feeds. They identified the optimal ranges for protein content or calf feeds. Moreover, they evaluated how nutrition interacts with different management and housing practices in dairy calves.

Specific objective 2: to quantify metabolic and molecular interactions that alter synthesis of milk.

Synthesis of milk and milk components is a function of numerous factors: supply of dietary and endogenously-derived nutrients, cooperation among non-mammary tissues such that the right mix and amount of nutrients are delivered to the mammary gland and finally the synthetic capacity of the mammary gland. This multistate team worked on these aspects at the organismal, tissue, cellular and molecular levels.

The CA team performed research on commercial dairies to evaluate the impact of variation in dietary nutrients and blood metabolites on the yield and composition of milk. This study involved cows followed throughout an entire lactation. Correlations were identified between blood non-esterified fatty acids (NEFA) and ketone body levels, and between NEFA and milk fat. This group also initiated studies to start understanding the basis for differences in overall efficiency of milk production focusing on mitochondrial efficiency as a predictor of energetic efficiency. One approach used was to vary copper and zinc as they both are known to alter mitochondrial function but these treatments had no effects on mitochondrial efficiency. A second group from MI took a genetic approach whereby they collected DNA and various measurements of efficiency (including residual feed intake) on thousands of dairy cows, with the long-term goal to identify genetic determinants controlling efficiency. They also conducted experiments to evaluate effects of various factors (energy density of diets, repeatability, etc.) on various indices of efficiency.

The WI team focused on the effects that fatty acids composition of dietary triglyceride on milk lipid composition. Milk short chain fatty acids are depressed by feeding triglyceride rich in linoleic acid whereas triglyceride rich in oleic acid and linolenic acid had smaller effects. On the other hand, triglyceride rich in oleic or palmitic acid elevated long chain fatty acids to a greater extent than those containing linoleic acid. The overall effects of palm oil were a combination of the effects of its 2 major fatty acids: oleic acid depressing short chain fatty acids while elevating long chain fatty acids whereas palmitic acid contributed to milk palmitic acid content and did not suppress short chain fatty acids. In summary, the effect of fatty acid composition of triglyceride on total milk fat yield was: palmitic acid > oleic and linolenic > linoleic.

The PA team described the time course of induction and recovery of diet induced milk fat depression. They showed that the key factor limiting recovery from milk fat depression was correction of dietary polyunsaturated fatty acids. Additionally, using a high palmitic acid supplement, they demonstrated efficient transfer of medium chain fatty acids into milk. Lastly, they uncovered a circadian rhythm in the synthesis of milk and milk component that is partially dependent on the timing of feed intake.

The MD team also worked lipid synthesis by the mammary gland. They demonstrated that providing short and medium chain fatty acids partially alleviated diet induced milk fat depression. Further, they showed that the trans-7 C18:1 fatty acid is another rumen biohydrogenation intermediate capable of inducing milk fat depression. Using mammary cell culture, peroxisome proliferator-activated receptor-gamma (PPARGs) was identified as a potential regulator of milk fat synthesis. However, a PPARG agonist failed to restore lipid synthesis during CLA induced milk fat depression, arguing against the involvement of this transcription factor under these conditions. The IA team found that specific genetic variants were associated with the synthesis of milk with different fatty acid compositions, suggesting that cows that produce healthier milk can be selected.

The efficiency of nitrogen utilization in ruminants, including lactating dairy cattle, is low compare to non-ruminants. To address the rumen contribution to this problem, MD researchers investigated the role of individual volatile fatty acids in regulating urea-N recycling, N utilization and gluconeogenesis in a growing sheep model. Overall, continuous infusion of butyrate or propionate did not alter urea-N recycling to the rumen, as hypothesized by others. Rather, providing propionate in a pulsatile manner improved N retention by reducing amino acid catabolism to urea.

Two teams focused on the supply of amino acids to the mammary gland and its effect on mammary protein synthesis. The KS team tested popular approaches of feeding rumen-bypass amino acid sources and observed a generalized lack of responses. These results pointed out to a lack of understanding of amino acid utilization by the mammary gland. The latter was one of the questions addressed by the VT group. They generated a large data set of responses to varying concentrations of individual essential amino acids, glucose, acetate, and insulin in mammary cell culture. They also assessed interactions among each of these nutrients and their effects on the mTOR pathway, which is closely linked to rates of casein synthesis. The VT team also assessed *in vivo* responses in milk protein synthesis to dietary manipulations of energy and metabolizable protein supply and essential amino acid content, and to infusions of starch, casein, insulin, and individual amino acids. Both the PA and IN teams used corn-based diets lacking adequate lysine to probe aspects of amino acids metabolism. The IN team studied the effects of supplying increasing levels of lysine on expression of key catabolic enzymes in liver of dairy cattle. They discovered that lysine catabolism in liver is responsive to lysine and protein balance in early lactation and that this response shows greater sensitivity during protein and lysine deficiency. The PA team showed that targeted supplementation with rumen-protected amino acids (e.g., Lys, Met, and His) could alleviate the loss of milk production in dairy cows fed protein-deficient diets.

The liver is at the nexus of metabolic pathways generating glucose and other essential precursors for milk synthesis. The IN team focused on the metabolic and molecular regulation of two gluconeogenic enzymes, cytosolic phosphoenolpyruvate carboxykinase (PEPCK) and pyruvate carboxylase (PC). They demonstrated that propionate regulated PEPCK via transcriptional mechanisms, suggesting a feed forward response for gluconeogenesis in ruminants. Moreover, they showed that (PC) is critical in gluconeogenesis from lactate and maintenance of TCA cycle intermediates. Moreover, they discovered that fatty acids can induce PC transcription and and mapped a region of the gene promoter responsible for this mechanisms. Another team (IA) documented that exogenous administration of glucagon to early lactating cows could reduce the degree of fatty liver infiltration.

Adipose tissue metabolism plays a critical role in the establishment of a successful lactation. The WA team worked on transcriptional mechanisms regulating the flux of carbon in and out of adipose tissue. In a series of studies in collaboration with IL, they found that, in early lactation, genes encoding enzymes promoting lipid accumulation (e.g., lipoprotein lipase, acetyl-CoA carboxylase) were decreased to only 20 to 50% of prepartum levels. In contrast, genes encoding enzymes involved in lipolysis (e.g., hormone sensitive lipase) were either unchanged or only moderately increased. Thus, early lactation is supported by coordinated changes in adipose that favors lipid export.

Other aspects of lipid metabolism were the focus of 2 other groups. The KS team sought to understand the basis for the ability of niacin to improve lipid metabolism in dairy cows. They showed that the bovine niacin receptor is present not only in adipose tissue but also in liver, muscle, and nervous tissue. A subsequent study tested the benefit of a relatively high dose of encapsulated niacin in early lactating dairy cows. The results demonstrated the potential for niacin to prevent ketosis in early lactation, but raised a concern as it also reduced feed intake. The NY team focused on the discovery of novel hormones regulating lipid metabolism in liver and adipose tissue. They focused on the liver derived protein fibroblast growth factor-21 (FGF21) and on the adipokine adiponectin. They found that plasma FGF21 was nearly undetectable in late pregnancy but increased and stabilized at chronically elevated concentrations during the energy deficit of early lactation. In contrast, plasma adiponectin varied in quadratic fashion with the highest levels in late pregnancy followed by a reduction in early lactation. Globally, these data suggest these novel hormones participate in the coordination of liver and adipose tissue in the early lactating dairy cow.

The MI team extended its work on the impact of nutrition on mammary development in prepubertal dairy heifers. They showed that feeding more energy and protein to preweaned calves increased mammary development and subsequent milk production. In contrast, feeding more energy to post-weaned, prepubertal heifers impaired mammary development and decreased subsequent milk production; the latter could be alleviated by feeding diets with higher protein to energy ratio.

Specific objective 3: to use this knowledge of feed properties and metabolic and molecular quantitative relationships to challenge and refine precision feeding systems for dairy cattle.

Members of this project have extensive experience working with "Molly", the most comprehensive mechanistic and dynamic model of metabolism in the dairy cow. The original Molly framework, however, did not contain information at molecular levels and also lacked information in a number of other areas, including amino acids use by the mammary and rest of the body.

The WA group conducted several modeling experiments to challenge and improve the Molly model. For example, they included molecular data on lipogenesis and lipolysis in adipose tissue, as well as functions modeling IGF-I signaling and its effect on follicular growth, initiation of ovarian cycling, and degradation of estrogen and progesterone. Through modeling experiments, they showed that increasing rates of lipogenesis did not change milk production or feed intake, but decreased milk fat production and decreased the postpartum interval to first ovulation. In contrast, increasing rates of lipolysis did not change milk production but increased milk fat and increased the interval to first estrus. This model could be used to interpret genomic and transcriptomic data leading to changes in productive and reproductive efficiency. Moreover, the WA and VA groups joined forces to compare the predictions of enteric methane from the original and newer versions of Molly (MollyOrigen, Molly84 and Molly85). They concluded that the version of Molly (Molly85) predicted CH_4 production from grass fed dairy cows with acceptable accuracy.

The VA group improved Molly by modifying parameters representing digestive processes (ruminal and intestinal digestibility) and post-absorptive processes (mammary synthetic activity, gestational nutrient requirements, and hormonal regulation of nutrient partitioning). They also developed a model of mTOR signaling in the mammary gland and parameterized it with respect to total essential amino acid and insulin concentrations. The VA group also helped devise a model of phosphorus digestion with VA and WA collaborators. The model considered the varied digestion of phytate, non-phytate organic, and inorganic forms of phosphorus and could be used to derive estimates of phosphorus digestibility in future Dairy NRC models.

The CA group conducted multiple modeling experiments of both finite biological processes and whole animal data. For example, they evaluated various rumen stoichiometric models for their predictive potential when used in mechanistic models. They also assessed different models to minimize sampling bias when examining cell numbers and size of adipocytes. They developed a linear programming model for dairy cattle to optimize diet formulation when constrained under different environmental policy scenarios (methane emissions, excretion of nitrogen and minerals).
A new suite of models were developed for predicting methane emissions from lactating dairy cattle, dry cows and heifers using state-of-the-art statistical techniques based on reversible jump MCMC and Bayesian techniques. Finally, a structural hierarchical model was developed to assess energy metabolism in lactating dairy cattle and suggested that maintenance and the efficiency of lactation have increased over the last few decades.

The Provimi group evaluated the currently accepted nutrition models for neonatal calves in light of the data they generated under objective 1. This exercise showed significant gaps in knowledge of protein nutrition for calves and heifers.

IMPACT STATEMENTS:

Impact statements are given under each of the 3 specific objectives of the project.

Specific objective 1:

- Improvement to quantitative predictions of metabolism of protozoa and their interaction with other microbes in mechanistic models. Overall effects are improved fiber digestibility, maintenance of milk production with lower protein content of diets and reduced risk of milk fat depression.

- Increased productivity (and immune function) of primaparous cows near peak lactation through dietary chromium propionate.

- Predictable milk fat responses to lactation diets high in non-forage fiber through addition of small amounts of physically effective forage NDF.

- Distiller grains can be fed with all types of forages in lactating dairy cattle.

- Reduction of dietary starch and gains in overall feed efficiency by feeding distiller grains or other distiller grains by-products.

- Flaxseed (and other oils seeds) can be used to supplement protein and energy in lactation diets and may lead to improved reproduction.

- Addition of glycerol to transition cow diets has the dual benefits of reducing diet sorting and improving overall health.

- Inclusion of flaxseed (and other oils seeds) to lactation diets increases omega-3 fatty acids content of milk.

- Yeast products, medium-chain saturated fatty acids, and herbs or plant extracts can modify rumen fermentation in dairy cows such that nitrogen utilization efficiency is improved and methane emissions is reduced.

- Intake of milk replacer powder impacts digestibility of nutrients both during the milk fed and early post weaning periods.

- Demonstration that some have specific effects on health and some immune markers of neonatal calves.

Specific objective 2:

- Development of guidelines to feed and manage cows to increase mitochondrial (and feed) efficiency.
- Predictable effects of dietary fatty acids on *de novo* lipogenesis and total lipid secretion by the mammary gland.
- Recovery of milk fat on dairy farms affected by milk-fat depression by addressing and correcting excess dietary polyunsaturated fatty acids.
- Sparing of amino acids for gluconeogenesis through inclusion of propionate into the diet.
- Feeding or intra-ruminal infusions of butyrate and propionate have no impact on urea recycling in forage-based diets containing intermediate to medium levels of starch.
- Demonstration that determination of milk urea nitrogen is an effective tool to monitor feeding programs and to reducing excessive dietary protein.
- Demonstration that protein synthesis is regulated in the mammary gland, fostering efforts by experimenters and modelers to include this phenomenon in metabolic models.
- Feasibility of sustaining milk production and improving nitrogen efficiency by feeding rumen-protected limiting amino acids in the context of protein-deficient diets.
- Promotion of gluconeogenesis and overall health in dairy cows through understanding of transcriptional stimulation of the PEPCK gene by propionate and PC gene by specific fatty acids.
- Resolution of molecular mechanisms (gene transcription or post-translational modification of receptors and enzymes) regulating the flow of lipids in adipose tissue during lactation.
- Sustained responses to sodium salicylate suggest that inflammatory signals early in lactation may have a programming effect on lactation performance.
- Identification of fibroblast-growth factor-21 and adiponectin as regulators of metabolism at the onset of lactation.

Specific objective 3:

- Availability for researchers of metabolic models incorporating molecular mechanisms accounting for lipid flux in/out of adipose tissue.

- Development of a cell signaling model underpinning mammary amino acid metabolism that can be used to improve existing whole animal models of amino acid and protein metabolism.

- Determination that existing models poorly predict volatile fatty acid production, thus providing impetus to the research community to address this lack of knowledge.

- Parameterization of a model of phosphorus availability in ruminants allowing reduced phosphorus feeding and environmental loading.

- Development of a greenhouse gas quantification protocol that producers and policy makers can use to claim carbon credits in markets such as the California Greenhouse gas Reduction Program.

- Mechanistic lactation models for better management of lactating dairy herds.

- Development of methods to analyze adipocyte population so that proper inference can be reached regarding the biology of hypertrophy and hyperplasia of adipose cells.

- Demonstration through modeling that reduction in CH4 emissions by dietary manipulation may be extremely expensive and may result in an increase in nitrogen and mineral excretion.

- Development of improved equations to estimate enteric methane emissions from different classes of cattle allowing better estimates in national inventories and proper evaluation of mitigation options.

- Derivation of more precise estimation of maintenance and efficiencies of lactating dairy cattle for use by producers and experimentalists.

- Development of a ration formulation model to estimate impact of marginal changes to efficiency of use of amino acids in growing calves.

- Identification of intake independent factors that can be manipulated on farms to improve growth rate of neonatal dairy calves.

The individual teams have been extremely successful in leveraging the results obtained under this multistate project to obtain funding from national funding agencies. Members of this project have obtained as PI or Co-PI over 18 grants funded by various competitive USDA programs totaling over $15 million. When international and all other national grants are included, these numbers exceed 33 grants and $18 million. In addition teams have obtained over 53 grants or contracts from private foundations and various industry groups totaling over $3.7 million. Finally, members of this project are recognized leaders in their research areas. Between October 2007 and Sept 2013, they have been invited to speak at numerous national and international scientific meetings (> 67 invitations). Members of this project have also been invited speakers to a countless number of meetings attended by translational professionals (practicing dairy nutritionists, veterinarians, extension specialists, industry professionals, etc.), thereby effectively disseminating findings to the ultimate stakeholders, i.e., dairy producers.

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