OPTIMIZING RUMINAL FERMENTATION TO MAXIMIZE AMINO ACID AVAILABILITY

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Adequate amounts of properly balanced diets must be fed to dairy cows throughout the lactation cycle if cows are to produce milk at their maximum genetic potential. During the early stages of lactation, the demand for nutrients by the mammary gland are extremely great in high producing dairy cows. As cows go from a pregnant-nonlactating state to peak milk production of 40 kg or more daily, the energy, protein, and mineral requirements increase 200 to 300% as a direct result of mammary gland requirements for milk production (NRC, 1989). Therefore, the critical period in the lactation cycle with regard to nutrient supply to high producing dairy cows is from the time of parturition until peak milk production (Clark and Davis, 1980). If the proper amount and ratio of nutrients required for synthesis of milk and milk constituents are not supplied to cows, they will mobilize nutrients from body tissue in an attempt to meet the requirements of the mammary gland for milk synthesis. Large quantities of nutrients must be supplied in the proper ratios to achieve high milk production and to prevent health disorders.

A deficiency of any nutrient may decrease microbial protein synthesis in the rumen, passage of amino acids (AA) to the small intestine, and milk production by dairy cows, but the two nutritional factors that are most likely to be limiting are energy and protein (Clark, 1975; Clark and Davis, 1980; 1983). Progress has been made in identifying the components of energy and protein that may be limiting milk and milk component synthesis. Glucose is of high priority because of the central role that it has in mammary gland metabolism for the synthesis of lactose which is the major osmotic regulator that controls the volume of milk produced by dairy cows. Volatile fatty acids and AA must be in adequate supply and proper balance for maximum milk production to be attained. Volatile fatty acids provide energy and serve as precursors for synthesis of fatty acids and glucose. Amino acids are used predominately for protein synthesis but can be used as precursors for glucose synthesis or can be oxidized to provide energy.

Dairy cows consume crude protein (CP) to supply nitrogen (N) for microbial protein synthesis and to obtain AA for maintenance and milk production. Microbial protein synthesized in the rumen, dietary protein that escapes ruminal degradation, and endogenous protein contribute AA that pass to the small intestine. In ruminant animals, the quantity and quality of AA reaching the small intestine may bear little resemblance to those in dietary protein because of the extensive microbial fermentation that occurs in the rumen. Therefore, it is a challenge to balance the diet to meet the AA requirements of dairy cows.

Protein nutrition of dairy cows cannot be investigated properly unless energy and N utilization by the ruminal microbes and by tissues of cows are considered simultaneously. Unfortunately, the relationship between N and energy requirements for ruminal microbes and for cows is complex and not well understood. Furthermore, establishing an optimal ratio of N to energy in the diet fed to cows is complicated because two requirements must be met, one for

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the rumen microbes and another for the host cow (Clark and Davis, 1983; Oldham, 1984).

Availability of AA may be increased by increasing feed intake, optimizing ruminal fermentation and microbial growth, and supplementing protein or AA to the diet that will escape ruminal fermentation and pass to the small intestine (Clark et al., 1992). Microbial protein normally contributes the largest amount of CP that passes to the small intestine. It is essential that conditions in the rumen be optimized for growth of the ruminal microbes if AA flow to the small intestine and yields of milk and milk components are to be maximized (Hoover and Stokes, 1991). Dietary AA that escape ruminal fermentation should complement AA provided in microbial protein.

Availabilities of energy and N are the major determinants of the amount of microbial protein synthesized in the rumen and microbial AA passed to the intestine. Nitrogen utilized for microbial protein synthesis can be derived from ammonia, AA, or peptides. A mixture of structural and nonstructural carbohydrates is normally the best source of energy for growth of bacteria, because upon fermentation, carbohydrates yield more energy per unit weight than protein (Nocek and Russell, 1988). Energy provided in the diet as fat can be taken up by the ruminal bacteria but it does not supply energy that can be used for protein synthesis (Van Soest, 1982).

Numerous factors have been investigated in an attempt to determine their influence on ruminal fermentation, nutrient passage to the small intestine, and animal performance (Sniffen and Robinson, 1987; Clark et al., 1992). Factors to be considered in this paper are the effects of feed intake, forage:concentrate ratio in the diet, source and amount of carbohydrate and protein in the diet, and the effects of feeding fat.

Feed intake

The amount of feed consumed is the nutritional factor that limits animal performance when balanced diets are fed to high producing dairy cows. The quantity of dietary nutrients that escape ruminal fermentation and the amount of microbial protein that passes to the small intestine are increased by increasing feed intake. However, this may not be readily observed unless passage is measured over a wide range of feed intakes. Lynch et al. (unpublished data) fed dairy cows a diet that consisted of 40% alfalfa haylage, 40% corn silage, and 20% concentrate. The four dietary treatments were ad libitum intake and 88, 76, and 64% of ad libitum intake (Table 1). Cows consumed 12.1 to 18.1 kg of dry matter daily. Because cows were fed the same diet, increasing dry matter intake increased the intakes of organic matter (OM), neutral detergent fiber (NDF), and N. This resulted in a larger amount of OM and NDF being degraded in the rumen for each incremental increase in feed intake. As feed intake and ruminal digestibility increased, there was a decrease in ruminal pH. Passage of OM and NDF to the small intestine also increased as feed intake was increased. The linear increase in N intake resulted in a linear increase in nonammonia-nonmicrobial nitrogen (NANMN), microbial N, nonammonia nitrogen (NAN), and individual AA passage to the small intestine. Therefore, one of the most important mechanisms for increasing nutrient availability to the dairy cow is to increase feed intake. The increase in nutrient availability is the result of both increased microbial

Table 1. Effects of feed intake on ruminal digestion and nutrient passage to the small intestine of dairy cows.

	Dry matter intake, kg/d			
Item	12.1	14.2	15.9	18.1
Digested in rumen				
OM (True), kg/d	5.4	6.1	6.9	8.4
NDF, kg/d	1.0	1.2	1.4	1.7
Nitrogen, g/d	303	356	397	453
Ruminal pH	6.57	6.45	6.40	6.23
Passage to duodenum				
OM, kg/d	7.6	9.2	10.3	11.0
NDF, kg/d	3.6	4.1	4.5	5.0
NANMN, g/d	148	138	156	188
Microbial N, g/d	184	234	269	287
NAN, g/d	332	373	425	475
Amino acids				
Essential, g/d	759	856	952	1071
Nonessential, g/d	816	932	1025	1160
Total, g/d	1574	1788	1978	2231

Lynch et al. (unpublished data).
OM = organic matter; NDF = neutral detergent fiber; NANMN = nonammonia, nonmicrobial nitrogen; N = nitrogen; NAN = nonammonia nitrogen.

digestion in the rumen and a larger amount of dietary nutrients escaping ruminal fermentation.

Robinson et al. (1985) fed a diet that contained 65% chopped grass-legume hay and 35% concentrate to Holstein cows. Feed was offered to provide 6 to 17 kg of OM daily. As OM intake and OM fermented in the rumen were increased, more total bacterial N passed to the small intestine. Furthermore, as OM intake increased, more bacterial N passed to the small intestine per unit of OM apparently digested in the rumen.

The quantity of microbial N that passes to the small intestine and microbial N passage per unit of OM fermented in the rumen appears to be greatest when dairy cows consume large amounts of feed that is high in carbohydrates. This can probably be attributed to faster growth of the microbes, reduced maintenance requirements of the microbes, a faster passage of digesta and microbes from the rumen, and decreased recycling of energy and N within the rumen because of decreased cell lysis. Therefore, data collected from animals eating small amounts of feed should not be extrapolated to animals eating large amounts of feed because both passage of microbial cells to the small intestine and efficiency of bacterial growth may be greater in animals consuming large amounts of feed with a high carbohydrate content. Furthermore, increasing passage from the rumen may increase the escape of

proteins with a high degradability in the rumen more than the escape of proteins with a low degradability.

Forage to concentrate ratio in diet

Altering the ratio of forage to concentrate in the diet also has been suggested as a mechanism of synchronizing the availabilities of energy and protein to maximize the amount of microbial and dietary protein that passes to the small intestine. However, any effects observed may be related as much to the amount of OM fermented in the rumen as to the forage to concentrate ratio in the diet. Rode et al. (1985) fed mid-bloom alfalfa hay, ground corn, and soybean meal based diets to dairy cows. Alfalfa hay provided 24, 38, 58, and 80% of the diets. Their data indicate that the amount of bacterial N that passed to the small intestine was positively correlated with the amount of OM truly digested in the rumen. Bacterial N and NAN passage to the small intestine was maximized when the diet contained 38% forage and 62% concentrate. Microbial N passed to the small intestine per unit of OM truly digested in the rumen was greater for the high forage diet than for the high concentrate diet when a correction was made for the amount of dry matter consumed but was similar for all diets if corrections were not made for the amount of feed eaten.

Klusmeyer et al. (1991a) fed dairy cows diets that contained alfalfa haylage, corn silage, ground shelled corn, soybean meal, and fat. The alfalfa haylage and corn silage supplied 50 or 67% of the dry matter in the diet. Cows fed the diet that contained 50% forage consumed more OM than cows fed the diet that contained 67% forage (Table 2). Nitrogen intake, OM truly digested in the rumen, and ruminal ammonia concentrations were not affected by amount of forage in the diet. More NANMN passed to the small intestine when the diet that contained 50% forage was fed probably because of the greater OM intake and because of the larger amount of corn in this diet. Feeding the diet that contained 50% forage slightly decreased microbial N passage to the small intestine which offset the increased passage of NANMN and resulted in no difference in NAN passage to the intestine when diets that differed in forage to concentrate ratio were fed to the cows. Because there were no differences between treatments for OM truly digested in the rumen and microbial N flow to the small intestine, efficiency of microbial N passage to the small intestine was not different between diets. Passage of individual AA to the small intestine also was not altered significantly by feeding different amounts of forage to the cows.

These data suggest that the amount of energy released from OM truly fermented in the rumen is the factor that probably limits growth of ruminal microbes when most diets are fed to obtain maximum milk production and that more microbial protein and less dietary protein pass to the small intestine when OM fermentation is increased in the rumen.

Table 2. Effects of forage to concentrate ratio in the diet and Ca-LCFA on intake, ruminal fermentation and nutrient passage to the small intestine of lactating cows.

	Treatments			
	50% forage		67% forage	
Item	No Ca-LCFA	Ca-LCFA	No Ca-LCFA	Ca-LCFA
OM intake, kg/d	23.3	22.0	22.4	21.0
N intake, g/d	741	691	715	679
OMTD, kg/d	10.9	8.7	10.8	9.6
Ruminal NH_3, mg/dl	12.6	13.2	12.3	13.3
Passage to duodenum				
Microbial N, g/d	313	297	336	313
NANMN, g/d	357	372	344	314
NAN, g/d	671	668	681	627
Microbial N/OMTD, g/kg	29.0	35.4	34.2	33.0

Klusmeyer et al. (1991a).
Ca-LCFA = Calcium salts of long chain fatty acids; OM = organic matter; N = nitrogen; OMTD = organic matter truly digested in the rumen; NH_3 = ammonia; NANMN = nonammonia, nonmicrobial nitrogen; NAN = nonammonia nitrogen.

Source and amount of carbohydrate in diet

Attempts have been made to synchronize energy and protein availability in the rumen by feeding dietary ingredients that differ in rate and extent of ruminal degradation. Hoover et al. (1990) tested the hypothesis of synchronizing the release of energy and N from the diet by balancing the diet for nonstructural carbohydrates and ruminally degradable protein. Diets formulated to be low in nonstructural carbohydrates and degradable protein decreased the intakes of dry matter, nonstructural carbohydrates, CP, and degradable protein. Ruminal digestion of dry matter and nonstructural carbohydrates also were decreased when the diet low in nonstructural carbohydrate and degradable protein was fed to the cows. Ruminal ammonia concentrations appeared to be adequate but were decreased for the diet low in nonstructural carbohydrates and degradable protein. Feeding the diet that was low in nonstructural carbohydrates and degradable protein decreased microbial N flow to the small intestine but increased feed N flow resulting in similar amounts of total N passing to the small intestine. Efficiency of microbial protein synthesis and passage to the small intestine was similar for all diets.

The quantity of microbial protein that passes to the small intestine has been reported to be affected by the type of starch fed to dairy cows. Oldham et al. (1979) fed dairy cows 14 to 15 kg per day of a barley or corn based concentrate and hay in ratios of 60:40 or 90:10. The quantity and efficiency of passage of microbial protein to the small intestine were greater for cows fed barley than corn at both ratios of concentrate to hay. Because of the

greater passage of microbial protein, total NAN flow to the small intestine also was greater for cows fed barley.

McCarthy et al. (1989) fed a total mixed diet that consisted of 45% forage and 55% concentrate that was either corn or barley based and formulated to contain 15% crude protein. Organic matter intake in this trial was greater than in most previous experiments and averaged 22.2 kg/d for corn based diets and 19.3 kg/d for barley based diets. Starch and N intakes were greater when corn was fed compared with barley because of the increased OM intake. When barley was fed, OM truly digested in the rumen was increased and ruminal ammonia concentrations were decreased. Feeding corn increased passage of OM, starch, NAN, and NANMN to the small intestine compared with feeding barley. The increased passage of NANMN was probably because of the low ruminal degradability of protein in corn compared with protein in barley and because of the greater feed intake when corn was fed compared with barley. The amount and efficiency of passage of microbial protein to the small intestine were not affected by the source of cereal grain in the diet. When cows were fed corn, more threonine, methionine, isoleucine, leucine, phenylalanine, and histidine passed to the small intestine, but source of cereal grain did not affect passage of valine, lysine, and arginine.

The relative abilities of grains to escape ruminal fermentation and to supply energy for microbial growth may be modified by their interactions with amount of feed intake, type and physical form of the feed, and the forage to concentrate ratio in the diet. Feeding the same source of grain with different forages or to cows consuming different quantities of the same feed may result in different quantities of microbial protein and dietary nutrients passing to the small intestine when expressed as amount per day or per unit of OM fermented in the rumen. Additional experiments are needed with animals eating large amounts of feed to determine the effects of feeding different sources of carbohydrates and CP on synchronizing energy and N availability in the rumen for maximizing microbial growth and nutrient passage to the small intestine.

Source and amount of nitrogen in diet

A deficiency of N in the rumen will depress both OM degradation and microbial protein synthesis. The majority of ruminal bacteria prefer to use ammonia as the source of N for growth (Bryant, 1974) and they are very efficient scavengers of ammonia (Schaefer et al., 1980).

Klusmeyer et al. (1990) fed dairy cows a total mixed diet of 60% corn silage and 40% concentrate that contained 11 or 14.5% CP on a dry basis. The cows consumed over 21 kg of dry matter or about 20 kg of OM daily. Nitrogen intake was greater when the 14.5% CP diet was fed compared with 11.0% CP and this significantly increased ruminal ammonia concentrations (8.0 vs. 2.2 mg/dl ruminal fluid). Organic matter truly digested in the rumen and microbial N passage to the small intestine were not significantly affected by CP content of the diet. These data suggest that a mean value of 2.2 mg of ammonia/dl of ruminal fluid was adequate for maximizing OM fermentation and microbial protein synthesis and that the amount of OM fermented in the rumen is more directly related to the amount and efficiency of microbial protein synthesis than is the ammonia concentration if it is above 2 to 3 mg/dl of ruminal

fluid. Feeding the diet that contained 14.5% CP doubled the amount of dietary N that passed to the small intestine which significantly increased passage of NAN and individual AA to the small intestine. Therefore, feeding the additional protein was beneficial for increasing the supply of AA to the small intestine because larger amounts of dietary protein escaped ruminal degradation even though microbial protein synthesis was not increased.

There is now evidence that AA and peptides are important sources of N for ruminal bacteria. Under normal conditions of feeding, large amounts of N used for growth by the bacteria can be derived from sources other than ammonia (Steinhour and Clark, 1981). The importance of AA N for growth of ruminal bacteria in batch cultures has been shown using isonitrogenous substrates that contained various ratios of urea N and AA N (Maeng et al., 1976; Maeng and Baldwin, 1976a,b). Replacing urea N with isonitrogenous quantities of AA N increased both microbial protein production and the energetic efficiency of microbial growth. These data indicate that not only can AA N be used by ruminal bacteria, but that it is required for maximizing microbial growth and efficiency of ruminal fermentation. If there is a deficiency of ammonia, AA, or peptides for microbial growth, the ruminal fermentation may become uncoupled and the microbes may continue to degrade OM to obtain energy but microbial protein may not be synthesized because availabilities of energy and N are not synchronized. Therefore, both microbial protein synthesis and efficiency of microbial protein synthesis may be depressed.

Feeding protein sources that have been reported to be highly degradable in the rumen have increased both the amount and efficiency of flow of microbial N to the small intestine compared with feeding protein sources that have been reported to be less degradable in the rumen. McCarthy et al. (1989) compared soybean meal and fish meal as the source of supplemental protein for dairy cows. Intakes of OM and N, the amount of OM truly digested in the rumen, and passage of NAN, NANMN, and AA to the small intestine were not affected by source of protein. Feeding soybean meal significantly increased passage of microbial protein to the small intestine and slightly improved efficiency of microbial protein flow to the small intestine. The improved microbial N passage may be attributed to an increased availability of ammonia, AA, or peptides in the rumen. However, there was little difference in the quantity of NANMN that escaped ruminal degradation. In this experiment as in most other experiments, the effects of AA and peptides, if any, on microbial growth were confounded with ruminal ammonia concentrations, and in this experiment, the ruminal ammonia concentrations also were low averaging 2 to 3 mg/dl of ruminal fluid.

Similar findings have been observed by Klusmeyer et al. (1991b) when soybean meal and fish meal were compared in the diet (30% alfalfa haylage, 20% corn silage, 50% concentrate) of dairy cows (Table 3). Organic matter and N intakes, OM truly digested in the rumen, and passage of NAN, NANMN, and individual AA to the small intestine were not affected by source of protein. Passage of microbial N to the small intestine was increased when soybean meal was fed compared with fish meal but source of protein did not affect the efficiency of microbial protein synthesis. Ruminal ammonia concentrations averaged 13 and 11 mg/dl of ruminal fluid, respectively, when soybean meal and fish meal were fed to the cows and should not have been deficient for microbial growth. Therefore, the increased passage of microbial N to the small intestine may have been associated with increased

Table 3. Effects of source of protein and Ca-LCFA on intake, ruminal fermentation, and nutrient passage to the small intestine of lactating cows.

	Treatments			
	Soybean meal		Fish meal	
Item	No Ca-LCFA	Ca-LCFA	No Ca-LCFA	Ca-LCFA
OM intake, kg/d	22.7	21.4	21.1	20.1
N intake, g/d	725	680	686	650
OMTD, kg/d	10.0	8.3	9.2	7.6
Ruminal NH_3, mg/dl	12.6	14.2	11.0	12.0
Passage to duodenum				
Microbial N, g/d	340	325	284	303
NANMN, g/d	335	324	343	342
NAN, g/d	675	649	627	646
Microbial N/OMTD, g/kg	35.3	41.0	31.3	41.5

Klusmeyer et al. (1991b).
Ca-LCFA = Calcium salts of long chain fatty acids; OM = organic matter; N = nitrogen; OMTD = organic matter truly digested in the rumen; NH_3 = ammonia; NANMN = nonammonia, nonmicrobial nitrogen; NAN = nonammonia nitrogen.

availabilities of AA and peptides from protein degradation in the rumen and (or) to a better synchronization of the release of energy and N fractions when dietary ingredients were degraded in the rumen, both of which may have stimulated microbial protein synthesis.

These data suggest that improvements in microbial protein synthesis may be attributed to increased availabilities and (or) an improved synchronization of ammonia, AA, and peptides with energy when degradable protein was added to the diet compared to other proteins that have been reported to be less degradable in the rumen.

Effects of feeding fat

To provide energy required to produce large amounts of milk, it has become a common practice to include fat in the diet of high producing dairy cows. If fat is to be used successfully in the diet of dairy cows it must not alter significantly ruminal fermentation or decrease the availability of nutrients required for milk production. Calcium salts of long chain fatty acids (Ca-LCFA) have been reported to be inert in the rumen (Grummer, 1988; Schauff and Clark, 1989) and to provide energy that can be used for production of milk.

Klusmeyer et al. (1991a) fed unsupplemented or Ca-LCFA supplemented (4% of dry matter intake) diets that contained 50 or 67% forage to investigate the

effects of Ca-LCFA on ruminal fermentation and passage of nutrients to the small intestine of lactating cows. Organic matter intake, N intake, and OM truly digested in the rumen were decreased by feeding Ca-LCFA, but ruminal ammonia concentrations and passage of NANMN, microbial N, and NAN to the small intestine were not altered significantly (Table 2). Passage of methionine and leucine to the small intestine were decreased significantly and passage of other AA were decreased numerically when Ca-LCFA were fed to the cows. The depressed OM digestion in the rumen and slightly lower passage of N components to the small intestine were probably the result of decreased feed intake, less carbohydrate being included in the diet, and fatty acid digestion occurring postruminally. Efficiency of microbial protein synthesis was not altered significantly but was numerically greater when Ca-LCFA were fed to the cows.

In a second experiment, Klusmeyer et al. (1991b) fed a total mixed diet that contained 30% alfalfa haylage, 20% corn silage, and 50% concentrate on a dry matter basis to determine the effects of Ca-LCFA on ruminal fermentation and nutrient passage to the small intestine of lactating dairy cows. Ca-LCFA were fed as 4% of the dietary dry matter and replaced corn in the diet. Feeding Ca-LCFA decreased OM intake 1.1 kg/cow/d and N intake about 40 g/cow/d (Table 3). Organic matter truly digested in the rumen was decreased and ruminal ammonia concentrations were increased when cows were fed Ca-LCFA, but passage of microbial N, NANMN, NAN, and individual AA were not altered significantly. Efficiency of microbial protein synthesis was improved when Ca-LCFA were fed and the improvement can be attributed to a smaller quantity of OM being digested in the rumen without decreasing microbial N passage to the small intestine.

Feeding unprotected fat has been reported to decrease the number of protozoa in ruminal fluid (Sutton et al., 1983; Tamminga et al., 1983) which may improve efficiency of microbial growth because of reduced recycling of bacterial N resulting from engulfment of bacterial cells by protozoa. Although Ca-LCFA are relatively inert in the rumen, they may decrease protozoa numbers because unsaturated fatty acids in Ca-LCFA are not completely protected from biohydrogenation (Zhiguo et al., 1989).

CONCLUSIONS

These data suggest that ruminal fermentation and the passage of microbial N and NANMN to the small intestine of dairy cows are affected by feeding management, feed intake, and the amount, type, and source of energy and crude protein in the diet. Additional experiments are needed with high producing cows that are eating large amounts of feed to identify the combinations of feed components that synchronize availabilities of energy and N and optimize digestion in the rumen, microbial protein synthesis, passage of nutrients to the absorption sites, and milk production. In these intensive trials, we must utilize cows that are eating and producing as we hope to have the target animal eat and produce if results are to be applied to feeding high producing dairy cows.

SUMMARY

Production drives feed intake which increases availabilities of energy and protein for production. The rate and amount of OM and CP digested in the rumen determine the rate and amount of microbial growth in the rumen when most diets are fed to dairy cows. This also influences the efficiency of microbial growth. Enhancing microbial growth in the rumen increases the supply of microbial protein to the small intestine and production of volatile fatty acids. A greater passage of solids and liquids from the rumen increases passage to the small intestine of both dietary nutrients that escape ruminal degradation and microbial protein. This may reduce recycling of N and energy in the rumen resulting in more microbial protein passing to the small intestine per unit of OM fermented. The greater passage of nutrients to the small intestine and enhanced production of volatile fatty acids increases the availability of nutrients that are most limiting for production. Therefore, nutrient availability can be enhanced by increasing feed intake, optimizing ruminal fermentation, and supplementing nutrients to the diet that will escape ruminal fermentation and complement endproducts of ruminal fermentation. Nutrient availability and production can be increased most efficiently if we consider all of these factors simultaneously.

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