

Amino acid nutrition: Demand and supply in forage-fed ruminants¹

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ABSTRACT: Amino acid requirements of cattle, particularly grazing cattle, scarcely have been studied. Limiting amino acids for growing cattle include methionine, lysine, histidine, leucine, and valine. Grazing cattle rarely demonstrate large performance responses to supplemental protein (provided ruminal N needs are met) due to the relationships between dietary energy supply, amino acid supply, and amino acid requirements. Amino acid requirements are related to dietary energy supply because protein deposition can be considered an energy-dependent process. Amino acid supply

also is an energy-dependent process as a result of ruminal synthesis of microbial protein. Thus, supply and demand for amino acids are both linked to dietary energy such that, under most grazing situations, deficiencies of amino acids are unlikely to be severe. Growing cattle fed grass silages may experience limitations in amino acid supply and, thus, are capable of responding to supplementation with ruminally undegraded protein. Predictions from the Cornell Net Carbohydrate and Protein System would support these conclusions.

Key Words: Amino Acids, Forage, Nutrient Requirements, Ruminants

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Introduction

This paper will address some of the factors that impact the amino acid (AA) requirements of forage-fed cattle as well as the supply of AA to the animal. At this time, the data are too limited to allow definitive conclusions about individual AA. Hopefully, this review will suggest areas of research where current information limits our ability to predict AA requirements for forage-fed animals in relation to the supply from forages and supplements. We also review production responses of forage-fed cattle to supplements containing ruminally undegraded protein (UIP). These responses are useful for determining whether AA supplies limit animal performance under various production conditions.

Amino Acid Requirements of Ruminants

Few measures of AA requirements for forage-fed ruminants are available. The Cornell Net Carbohydrate and Protein System (CNCPS; O'Connor et al., 1993) provides a framework for predicting AA requirements that demonstrates some of the factors that deserve consideration. Within the CNCPS, AA requirements are

separated into needs for maintenance, growth, gestation, and lactation; this section primarily focuses on nonpregnant, nonlactating animals. Maintenance requirements are based on previously published estimates of requirements for protein for scurf, endogenous urinary, and endogenous fecal losses. Maintenance protein needs are then converted to AA requirements using AA profiles of appropriate tissues (keratin for scurf and whole body for urinary and fecal losses). Protein requirements for growth are based on net-protein deposition and an efficiency of utilization; AA requirements are based on converting protein needs to AA needs using the AA profile of whole-body tissue. The efficiencies of utilization for individual AA are based on relationships between absorbed and deposited protein and are dependent on the animal's BW (efficiency = $0.83 - 0.00114 \times$ empty BW in kilograms).

Often, AA requirements are set for animals at their maximal performance. However, it is important to identify the factors that determine the maximal level of performance. In essence, AA requirements for maximal performance are defined at the point where some factor besides AA supply becomes limiting. The factors most likely to become limiting are energy supply and genetic capacity of the animal, but other circumstances such as a mineral or vitamin deficit could also limit performance. With the CNCPS, performance and, thus, requirements are based on protein deposition, which is based on the energy-allowable gain and the predicted-protein composition of that gain (O'Connor et al., 1993).

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For nonruminant animals, the relationships between energy supply, protein supply, and protein deposition of growing animals can be described in a relatively straightforward manner (Campbell et al., 1985). Protein (AA)-dependent phases of growth and energy-dependent phases of growth can be described. When energy is limiting, the animal will not respond (i.e., increase protein deposition) to the supply of additional protein. Thus, under energy-limiting conditions, the AA requirements of the animal have been met. Under energy-limiting conditions, the supply of additional energy, up to a point where AA supply, genetic capacity of the animal, or any other factor becomes limiting, will increase protein deposition. In essence, the supply of additional energy increases the animal's AA requirement. On the other hand, when adequate energy is available to the animal, protein deposition is linearly related to the supply of the most limiting AA, up to the point where energy or another factor limits performance. Thus, for a given level of energy supply, a specific requirement for AA can be determined. Greater supplies of energy, in the absence of other limiting factors, increase AA requirements.

For ruminants there is conflicting evidence of the existence of protein- and energy-dependent phases of growth, in part because relatively few studies have addressed this issue in a manner that can be clearly interpreted. There are relatively little data on protein-energy interactions in ruminants because dietary manipulations cannot be used to alter energy supply independent of the protein supply. Increases in dietary energy invariably increase protein supply as a result of synthesis of microbial protein in the rumen. Thus, to study energy-protein interactions, energy must be provided in a form that will not impact microbial fermentation; several approaches would include postruminal infusions of nonproteinaceous energy sources and ruminal supply of VFA. Intragastrically maintained animals or preruminants, wherein the intervening microbial population is removed or not yet developed, also are useful models for assessing energy-protein interactions. However, there are limitations to these models due to the low levels of performance typically observed for intragastrically maintained animals and concerns that preruminants may not be regulated metabolically the same as adult ruminants.

Gerrits et al. (1996) conducted an excellent study to consider protein- and energy-dependent phases of growth in preruminant calves. Graded levels of protein were provided to calves receiving two levels of energy. Protein- and energy-dependent phases were not observed. When calves were given additional protein, at either level of energy, protein deposition increased. However, when the energy supply to the calves was increased, even when protein supplies were considered deficient, there also were increases in protein deposition.

On the other hand, Lindberg and Jacobsson (1990), working with intragastrically maintained yearling

sheep, did observe responses in N balance that were consistent with the presence of protein- and energy-dependent phases of growth. Sheep were given graded levels of protein in conjunction with three levels of VFA provided as ruminal infusions. Low levels of protein supplementation yielded similar improvements in N balance at each of the three levels of energy, suggesting that performance was protein-dependent. However, responses to higher levels of protein supplementation were less for those sheep given the lowest energy supply, suggesting that performance was limited by energy when excess protein was available. In contrast, Hovell et al. (1983), working with intragastrically maintained lambs (4 to 6 mo of age), demonstrated that N retention increased when either energy or protein was supplemented.

A factor that may impact the energy-protein relationship is the physiological status of the animal. Ruminants near energy maintenance are capable of mobilizing body fat to supply the energy necessary for protein deposition (Fattet et al., 1984; Chowdhury et al., 1997). Asplund (1994) termed this response the "lipotropic effect." In addition to ruminants near maintenance, this effect can be demonstrated clearly in lactating animals.

Because body fat can be mobilized and used as an energy source, it can contribute to an effective energy-to-protein ratio greater than from the diet alone. Fat animals presumably would have a greater capacity for mobilizing fat than would thin ones. The lipotropic response may explain some of the differences among studies that have evaluated protein-energy relationships in ruminants, although the young calves in the study of Gerrits et al. (1996) that did not demonstrate protein- and energy-dependent phases of growth would be expected to have little body fat, such that the lipotropic effect would be unlikely to have modified greatly the effective energy-to-protein ratios.

Within set levels of energy supply, a number of studies have demonstrated that, under conditions of AA limitation, protein deposition (measured by growth or N balance) increases linearly in response to supplementation with a limiting AA until the requirement is met, at which point further increases are not observed (Campbell et al., 1997; Froidmont et al., 2000). This would seem to be a demonstration of protein-dependent phases of growth, although it is possible that the response to AA supplementation would be altered in the face of a different supply of energy.

The previous discussion does not provide much insight into AA requirements, but it does suggest that the energy supply to the animal must be considered. If the protein-dependent phase of growth was the only aspect that required consideration, AA requirements could be based solely on the observed level of protein deposition because energy status would not alter the efficiency of AA use. Under those conditions, the supply of energy would only be an important consideration in that it would be needed to support the expected level of protein deposition. However, if energy and protein

supplies interact to impact animal performance, assessment of AA requirements becomes very difficult because energy supply would alter the efficiency of AA use, and animals with the same amount of protein deposition could have different AA requirements.

Little research data are available to support or contradict the efficiencies of AA use predicted by the CNCPS. Research with methionine, which is often considered the first limiting AA for cattle, has demonstrated linear increases in protein deposition in response to methionine supplementation and efficiencies of use for protein deposition of 24% for 160 kg Holstein steers (Campbell et al., 1997), 43 to 58% for similar lightweight Holstein steers (Löest, 1999), 33% for 294-kg Limousin-cross steers (calculated from the data of Titgemeyer and Merchen, 1990), but only 12.5% for 315-kg double-muscle Belgian Blue bulls (Froidmont et al., 2000). From these data sets, it appears that factors beyond BW are involved in influencing the efficiency of methionine utilization for protein deposition. For some of these data sets, however, when N retention was regressed against methionine supply, the predicted maintenance requirement (i.e., methionine supply necessary for N retention = 0) was negative. This suggests that the efficiency of methionine use was nonlinear and that it was higher at low levels of methionine supply. If this were true, then use of a single coefficient for AA utilization across all levels of protein deposition would be invalid.

Limiting Amino Acid for Ruminants

A number of studies have measured responses of ruminants to single AA or intact proteins, but relatively few studies have thoroughly evaluated which AA are qualitatively important for growing ruminants. For lambs, Storm and Ørskov (1984) determined that microbial protein was most limiting in methionine, lysine, arginine, and histidine, and that the deficiencies of arginine and histidine were relatively small. Work with growing calves fed soybean hull-based diets, for which most of the metabolizable protein would be supplied by the ruminal microbes, suggests that methionine, lysine, histidine, and at least one of the branched-chain AA are limiting AA (Greenwood and Titgemeyer, 2000). Unpublished data from our laboratory have shown that leucine and valine are limiting, whereas isoleucine is not.

In general, forage proteins are extensively degraded within the rumen, such that most of the metabolizable AA supply is of microbial origin. One exception to this would be tryptophan, for which concentrations in forages are high relative to that in animal tissues (NRC, 1996); even in the face of extensive ruminal degradation, the forage would likely supply an appreciable quantity of tryptophan to the animal. No other essential AA is distinctly higher in forage than in animal tissue such that an unbalanced supply would result from ruminal escape of forage AA. Thus, it is likely that the

above listed AA would be most likely to limit performance of forage-fed ruminants.

Amino Acid Supply to Forage-Fed Ruminants

The supply of AA to a ruminant can be considered at several different levels. The first would be the diet, which, due to ruminal fermentation and the importance of microbial protein to post-ruminal AA supply, has little relationship to metabolizable AA supply. Another level of supply would be the metabolizable AA supply, which, if endogenous sources are considered minimal, can be considered the sum of intestinally digestible microbial and intestinally digestible undegraded dietary proteins. Another level of supply that might more accurately reflect the AA available for animal growth would be total splanchnic flux, which is the amount of absorbed AA that are released after metabolism by the gut and liver.

Several studies with sheep fed bromegrass hay have compared the effects of various supplements on AA supply as measured by portal and total splanchnic fluxes of α -amino N. Goetsch et al. (1994) fed sheep bromegrass hay (10.4% CP) and supplemented corn (0.5% of BW), soybean hulls (0.7% of BW), or a high-protein supplement (high UIP; 0.073% of BW). Because forage intake was not greatly affected by the supplements, total DMI were greater for the corn and soybean hull supplements. Total protein intake was greatest for the soybean hulls, followed by the UIP supplement, then the corn, and controls received the least digestible protein. Net fluxes of α -amino N across portal-drained viscera were increased above control equally by all three supplements. Numerically, the amounts of AA removed by the liver were increased by the soybean hull and UIP supplements. These changes resulted in numerically more AA being released from splanchnic tissues for the corn-supplemented lambs than for the other supplements, with controls being lowest. This points out that energy supply (source as well as amount) may impact the utilization of AA. In this case, although the corn and soybean hull supplements were designed to supply an equal amount of DE, the corn supplement provided more absorbable glucose than did the soybean hulls; this was one of various differences that could have contributed to the differences in AA utilization.

Ferrell et al. (1999) fed wethers bromegrass hay (4.3% CP) and supplemented them with only energy (cornstarch and molasses mix at 0.3% of BW) or with a combination of energy and one of three N sources: urea, soybean meal (source of ruminally degraded protein [DIP]), or a high UIP source. The energy supplement alone did not increase the release of α -amino N across portal-drained viscera, but it did increase uptake of AA by the liver. Thus, there were numerically fewer AA released from splanchnic tissues when only the energy was supplemented. These changes were associated with an increase in oxygen consumption by the liver. On the other hand, when the energy supplement was fed along

with any of the N sources, release of α -amino N across portal-drained viscera was increased, reflecting the greater supply of metabolizable protein. Uptake of AA by the liver when N was supplemented was similar to that observed when only energy was supplied, and release of AA by total splanchnic tissues was similar to controls when energy and N were supplemented together.

It is not easy to justify the different responses to energy supplementation in the studies of Goetsch et al. (1994) and Ferrell et al. (1999). However, forage qualities were different (10.4 vs 4.3% CP), and changes in intake in response to treatment were different. The wethers in the study by Goetsch et al. (1994) did not greatly change forage intake in response to supplement, so those sheep fed corn or soybean hulls had total dietary intakes greater than controls. Sheep in the study by Ferrell et al. (1999) also did not demonstrate large changes in forage intake in response to supplementation, which was somewhat unexpected considering the low-protein content of the forage, and total dietary intakes were similar among treatments. Nonetheless, these studies do demonstrate that interactions between energy availability and AA utilization can exist.

The liver is clearly the key site of degradation of essential AA, and it plays a key role in determining the supply of AA to extrahepatic tissues. It is particularly important because it has access to portally released AA prior to the rest of the body. From one perspective, it could be argued that the liver will determine the ability of the animal to deposit protein because it regulates the supply of AA. However, hepatic degradation of AA is regulated by substrate supply (i.e., the presence of AA not needed by the body for deposition). As discussed earlier, the amount of AA used by the body will be dependent upon the energy available to support protein deposition. Thus, a more appropriate perspective would be to consider the liver responsive to the needs of extrahepatic tissues and their ability to deposit proteins, rather than as the regulator that drives growth by metering the release of AA. In the studies of Ferrell et al. (1999), the increased removal of AA in response to increased gut supply, in the absence of additional energy, might reflect the supply of AA exceeding the animals' needs for deposition, which was energy limited. On the other hand, in the study of Goetsch et al. (1994), energy supply and protein deposition probably increased in concert with AA supply such that the additional AA were used for deposition and, thus, disposal by hepatic degradation was not necessary.

Taniguchi et al. (1995) also evaluated possible interactions between energy supply and AA utilization. Casein (200 g/d) and starch (800 g/d) were supplied ruminally or abomasally in a factorial arrangement to steers limit-fed alfalfa hay. The site of starch infusion had little impact on α -amino N release from the gut or on hepatic extraction of AA. However, when casein was supplied postruminally, where it could contribute to metabolizable protein supplies, the amount of α -amino

N released from the gut was greater than when it was supplied ruminally and fermented by ruminal microbes. Hepatic extraction of AA was also increased by postruminal casein, but the increased release from the gut was greater than hepatic extraction, so total splanchnic release was increased by postruminal casein. Interestingly, in contrast to our interpretation of the data of Goetsch et al. (1994), the site of starch infusion, and presumably the different endproducts of digestion absorbed by the gut, did not impact greatly the supply of AA to the body. This may be because the starch would provide glucogenic substrates either through direct absorption of glucose from the small intestine for the abomasal infusions or through ruminal fermentation to propionate. Because the total amount of energy provided was similar among treatments, this data set cannot be used to address the effects of energy level.

Krehbiel et al. (1998) conducted a study to evaluate the impact of infrequent supplementation on AA supply to ewes fed bromegrass hay (7.5% CP) and supplemented with soybean meal daily or once every 3 d. The supplemental soybean meal increased total dietary intake by 35%. Release of α -amino N across portal-drained viscera as well as hepatic extraction of AA was increased by soybean meal supplementation, with the response averaged over the 3-d period being similar for the two frequencies of supplementation. The increases in release of AA by the gut in response to soybean meal supplementation were greater than increases in AA uptake by the liver, leading to numerically more AA being released to the rest of the body. Day-to-day variation was increased by less frequent supplementation (i.e., gut release and hepatic extraction of AA were greatest on the day after supplementation for ewes fed every third day), but, across the 3 d, average fluxes were not impacted by frequency of supplementation. These data demonstrate, in mature ruminants, the ability of the body to respond metabolically to temporal variations in nutrient intake.

Implications for Practical Supplementation of Forage-Fed Ruminants

In general, the ratios of available protein to energy for various forages do not differ greatly because microbial protein production is directly related to fermentable energy. Also, forage protein concentration, and thus forage UIP, demonstrates a relationship to energy content. It has been suggested, as a result of these relationships, that AA rarely limit performance of ruminants. Asplund (1994) suggested that the yield of AA N from microbial fermentation is approximately 3.3 g/MJ of ME, and that the optimal ratio of protein to energy for the animal is 1 g AA N/MJ of ME. Clearly, this would imply that supplementation to increase AA supply would be unnecessary. However, data from Lindberg et al. (1990) and Gerritts et al. (1996) would suggest that the optimal ratio of protein to energy for the animal

Table 1. Nutrient supplies in relation to performance of cattle grazing various forages as predicted by the Cornell Net Carbohydrate and Protein System

Item	Forage				
	Grass silage	Spring ryegrass	Summer grass	June range	September range
Forage CP, %	16.0	24.2	15.0	11.0	8.5 ^c
Forage TDN, % ^a	69	82	73	67	62
658-kg dry cow, DMI = 13.1 kg/d					
	Supply/Requirement, %				
ME	111	130	119	107	93
MP ^b	126	198	184	138	116
Methionine	105	125	150	121	110
Lysine	119	155	171	135	116
589-kg lactating cow, DMI = 13.9 kg/d					
	Nutrient allowable milk, kg/d				
ME	10.3	15.6	12.1	9.3	6.6
MP ^b	9.7	21.1	20.0	12.1	8.2
Methionine	8.7	14.4	19.8	12.7	10.0
Lysine	8.0	14.6	18.5	11.6	8.7
200-kg steer					
DMI, kg/d	5.15	5.16	5.21	5.04	4.67
	Nutrient allowable gain, kg/d				
ME	0.54	1.03	0.71	0.43	0.13
MP ^b	0.48	1.10	1.07	0.60	0.34
Methionine	0.42	0.69	0.98	0.61	0.42
Lysine	0.40	0.74	0.97	0.58	0.39
400-kg steer					
DMI, kg/d	10.38	9.98	10.38	10.30	9.92
	Nutrient allowable gain, kg/d				
ME	0.74	1.24	0.91	0.61	0.31
MP ^b	1.02	2.24	2.18	1.26	0.76
Methionine	0.82	1.38	1.92	1.18	0.85
Lysine	0.80	1.48	1.91	1.14	0.79

^aAverage TDN content across animals.

^bMetabolizable protein.

^cCrude protein content of forage with urea added to meet ruminal N needs.

would be 1.5 to 2.3 g N/MJ of ME. Also, estimates of supply of absorbable AA N from microbial protein would suggest that a value of 1 g AA N/MJ of ME (based on 8.32 g absorbable AA N per kg TDN; NRC, 1996) would be closer to the reality than the estimate of 3.3 provided by Asplund (1994). Thus, in the absence of dietary UIP and of a lipotropic response, supplementation to increase AA supply theoretically would be of benefit.

In contrast, modeling exercises with the CNCPS (Release 4.0; Dept. of Animal Science, Cornell Univ., Ithaca, NY) suggest that for growing steers and pregnant cows the AA requirement is typically met when unsupplemented forages are fed (Table 1). For the modeling exercise, five forages were evaluated for four cattle types. The forages were selected from the feed database available with the computer program and were selected to range in protein content and energy availability. The September range was supplemented with urea to meet the ruminal N needs; the other forages fully met the predicted needs for ruminally available peptides and N. Intakes predicted by the program were used. Animal breed was selected to be a Hereford × Angus cross,

animal characteristics were selected to avoid thermal stress, and default settings were scarcely altered.

For gestating cows (250 d pregnant), all of the selected forages met the cows' needs for metabolizable protein, methionine, and lysine. All forages except the September range met the cows' energy (ME) needs. For pregnant cows consuming grass silage and spring ryegrass, methionine supplies relative to requirements were slightly lower than those for ME, which may suggest that under conditions of slightly lower intakes methionine could become limiting.

Milk production entered into the computer program for lactating cows was 9.0 kg/d. This relatively high level of production for beef cows was selected to generate high requirements in support of lactation. For spring ryegrass, summer grass, and June range, supplies exceeded the milking cows' requirements for metabolizable protein, methionine, and lysine. For grass silage, both methionine and lysine supplies were deficient and would have been most limiting for lactation. For September range, metabolizable protein and lysine

were predicted to be deficient, but energy supply would have been most limiting.

Lightweight calves (200 kg, 9 mo of age) were predicted to have energy-allowable gains greater than those allowed by supplies of methionine and lysine when either the grass silage or spring ryegrass was consumed. For the other three forages, gains would have been restricted by energy availability. In contrast, heavier weight steers (400 kg, 15 mo of age) were more limited by energy than by protein, methionine, or lysine for all five forages. This shift in the most limiting nutrients as the steers become larger is related to the greater energy-to-protein requirement for growth by the heavier steers.

Across the different animals, it is interesting to note that the forages that supplied the highest CP levels (grass silage and spring ryegrass) were most likely to lead to protein or AA deficiencies. In the case of the grass silage, this can be attributed to the low amounts of UIP supplied by the forage as well as yields of microbial protein less than for some of the other forages. For the spring ryegrass, the lower supplies of metabolizable protein were related mostly to low yields of microbial protein.

Responses of Forage-Fed Ruminants to Undegraded Protein

General Considerations

Despite our inability to predict accurately the quantitative requirements for AA, there is information that can be used to determine the importance of supplementing forage-fed cattle to meet AA needs. These studies involve increasing the supply of AA through the use of supplements containing UIP, which supplies usable AA directly to the small intestine. If performance (protein deposition, growth, or milk production) improved in response to UIP supplementation, this would imply that the basal supplies of AA (i.e., that supplied by the UIP of the forage and by the ruminal microbes) were insufficient to meet the animal's needs. However, before this interpretation can be considered valid, we must be relatively assured that the UIP supplement increased AA supply but did not greatly impact forage utilization (and thereby alter energy supply).

Supplements containing UIP usually contain other nutrients as well, particularly DIP. Even a pure source of UIP (such as protein that was provided to the animal postruminally) can act as a DIP source via N recycling (NRC, 1996). Thus, the effects of DIP on ruminal fermentation and forage utilization must be considered. In cases where the DIP needs of the ruminal microbes have been fully met, either by DIP supplied by the forage itself or by supplementation of a concentrated source of DIP, responses to UIP are likely due to the increase in the postruminal supply of AA, although there are situations where hormone-like activities of intact proteins could alter digestion (Froetschel, 1996).

Comparison of performance of UIP-supplemented cattle with that of unsupplemented controls will only be a valid evaluation of AA status if the forage contains adequate DIP to optimize its utilization. In cases where the forage contains inadequate amounts of DIP, the appropriate control supplement would be designed to meet the DIP requirements of the forage. Then, additional UIP could be supplied, and responses above those observed to DIP supplementation would be considered indicators of an AA insufficiency. In cases where UIP replaces DIP on an equal N basis, lack of response to the UIP source may be because AA supply has not been changed. Although the UIP supplies absorbable AA, the lowered DIP supply may limit microbial AA production such that the total supply of AA is not greatly modified. Also, excessive quantities of DIP may lead to depressions in performance as a result of excessive amounts of ammonia being absorbed from the rumen (Lobley et al., 1995). Under those conditions, replacing DIP with UIP may exert a positive effect by ameliorating the effects of excess ammonia.

Production Studies with Cattle

Obviously, there are many possible management systems that use different forages and types of cattle and that have varying expectations for performance. It is difficult to interpret responses to changes in AA supply when ruminal N needs have not been met by the control treatment because forage utilization may be impacted. The following sections will consider, within some different management systems, responses of cattle to supplementation with UIP under conditions where changes in forage utilization (i.e., intake and digestion) did not appear likely.

Pregnant/Lactating Beef Cows on Pasture. Cows that consume poor-quality, low-protein forages will respond to supplementation with DIP (Köster et al., 1996). Much of this response is a result of increases in forage digestion and intake as a result of correcting the ruminal N deficiency. Research described below also indicates that in some cases small responses in weight gain and milk yield are possible with supplementation of UIP in addition to DIP.

Pregnant beef cows grazing native range in Montana during winter (forage CP was 4.6 and 7.2% during the 2 yr of the study) were supplemented with soybean meal (a source of DIP) or with mixtures of soybean meal and either blood meal or corn gluten meal (sources of UIP) with the predicted amount of DIP being equal among the treatments (Miner et al., 1990). Over the trials, which lasted around 80 d, cows fed the UIP sources tended to gain an average of 10.6 kg more weight and lose 0.4 less in body condition score (scale of 1 to 10) than those fed only soybean meal. However, for multiparous, pregnant cows grazing dormant tall-grass pastures, supplementation with UIP in amounts greater than that provided by a base supplement de-

signed to meet DIP requirements led to no changes in weight gain or pregnancy rates (Olson, 1998).

Dhuyvetter et al. (1993) evaluated postpartum supplementation of beef cows grazing native range in Montana with supplements containing 25 or 50% of the protein as UIP. For early-calving cows (March 4 to 20) that received access to 10.5% CP hay, supplementation with the higher level of UIP (from March 25 through May 30) led to 40 kg less loss of BW, but subsequent calf gains and percentages of cows rebreeding were not affected. Late-calving cows (March 20 to April 23), when offered the same supplements, showed no response to UIP, which the authors attributed to a deficiency of DIP for the supplement with 50% UIP; the late-calving cows did not receive access to the hay, which contained more protein than did the range forages.

Hibberd et al. (1988) also evaluated the effects of increasing UIP content in supplements for lactating beef cows maintained on dormant native grass. Cows fed UIP at the expense of DIP tended to lose less weight (6 kg less over 83 d) and had greater milk production, which resulted in slightly greater gain of calves (3.5 kg). Energy for increased milk production may have been provided by mobilization of body fat (lipotropic effect), although differences in body condition change among treatments were not present to support that conclusion.

For lactating cows grazing higher quality forages, UIP supplementation has been shown to have little effect on weight gain, milk production, and calf gain. For cows grazing smooth brome (17 to 25% CP) and big bluestem (11 to 17% CP), replacing an energy supplement with various levels of UIP (mix of blood meal and corn gluten meal) yielded few effects (Blasi et al., 1991). Similarly, lactating cows and heifers grazing rye-ryegrass overseeded Coastal bermudagrass pastures (25% CP) with access to Coastal bermudagrass hay (8% CP) did not demonstrate meaningful differences in cow or calf performance in response to UIP supply, although UIP supplementation increased pregnancy rate as a result of decreasing the percentage of heifers that did not return to estrus during the breeding season (Triplet et al., 1995). Wiley et al. (1991) similarly observed that forage-fed heifers supplemented with UIP postpartum had reduced postpartum intervals. In that study, heifers were fed a diet based on medium-quality grass hay (10% CP), and control heifers (low UIP) received 125% of predicted CP requirements, whereas the UIP-supplemented heifers received 180% of predicted CP requirements. Rusche et al. (1993) also observed numerically higher conception in heifers receiving either 100 or 150% of estimated protein needs from diets based on prairie hay when the UIP content of the diet was increased.

Across these studies, the differences in performance in response to UIP supplementation were relatively small, suggesting that AA deficiencies of cows receiving adequate DIP were relatively small or that they were able to respond to the challenge of the deficiency by

mobilizing body tissues. It is important to note that, for cows on poor-quality forages, supplemental DIP is required to meet ruminal needs, and all practical DIP sources except urea will supply some UIP as well as the DIP. Thus, the basal supply of metabolizable AA will typically be more than that supplied only by the forage and the microbes. With pregnant or lactating cows, small changes in performance are relatively unimportant from an economic standpoint as long as reproductive efficiency is not impaired and cows have an opportunity during the grazing season to replenish lost body reserves. Thus, heifers would seem more likely than multiparous cows to respond to UIP supplementation postpartum.

Growing Steers and Heifers. Growing cattle are fed a wide range of forages, and expected gains can vary greatly depending on the energy content of the forage. Within the constraints of the available energy, the question is whether metabolizable AA supply is adequate. This question has been most effectively addressed by performance studies wherein metabolizable protein supply has been increased by supplementation with a UIP source.

Growing cattle fed high-quality warm-season grasses have, in some cases, had greater weight gains when supplemented with a source of UIP compared to an energy control. Steers grazing warm-season grasses over the summer showed an increase in gains from 0.91 kg/d for the energy control to 1.01 kg/d when 200 g/d UIP was supplemented (Hafley et al., 1993). However, heifers grazing similar pastures did not show responses to supplementation with UIP, but did demonstrate rather modest increases in gain when a supplement high in DIP was supplemented (gains increased from 0.94 to 1.03 kg/d; Hafley et al., 1993). Karges et al. (1992) also demonstrated a small increase in daily gains (from 1.02 to 1.11 kg/d) when steers were supplemented with 200 g/d UIP, and these authors stated that the differences in gains were maintained through a subsequent finishing period. In contrast, Rogers et al. (1996) observed no response to additional UIP when steers grazing bermudagrass (20% CP) were supplemented with UIP. Grigsby et al. (1989) also failed to observe responses to addition of UIP to cooked molasses blocks or of AA to dry supplements fed to growing steers and heifers grazing bermudagrass (12% CP forage capable of supporting 0.5 kg/d gains), although it should be noted that the base supplements would have provided some UIP to the cattle. For steers and heifers grazing bahiagrass pastures (supplemented with stargrass hay as pasture availability declined), addition of feathermeal to a urea-containing liquid supplement improved gains by about 0.1 kg/d (Pate et al., 1995); forage quality could be considered low because cattle supplemented with the urea-containing supplement had average gains of only 0.04 kg/d. Brown and Pate (1997) demonstrated that cattle fed ammoniated stargrass hay (capable of supporting gains of 0.22 kg/d when supplemented with a urea-containing liquid supplement)

would grow faster ($ADG = 0.54$ kg/d) when supplemented with either feathermeal (a high-UIP source) or cottonseed meal (a low-UIP source). Thus, it is possible that the response to protein supplementation that was observed by Brown and Pate (1997) was a result of changes in ruminal fermentation and energy supply.

Supplementation of cattle grazing cool-season grasses with UIP sources has also led to modest increases in growth of steers. Steers grazing smooth brome through May and June demonstrated increases in gains from 0.91 kg/d to an average of 1.03 kg/d when 230 or 340 g/d of protein (high percentage of UIP) was supplemented (Anderson et al., 1988) and from 0.72 to 0.83 when 227 g/d protein was supplemented (Goedeken et al., 1987). However, gains were increased more when an energy source (1.36 kg/d corn bran) was supplemented than when the UIP sources were provided. Similar improvements in gain (0.11 kg/d) were observed for steers grazing smooth brome in the fall (September to November) when they received at least 110 g/d protein from high UIP sources (Anderson et al., 1988). However, greater improvements in gain (from 0.67 to 0.90 kg/d) were observed for steers grazing smooth brome through June and July, and responses to energy supplements (corn and corn bran) were less than to the UIP.

Responses to UIP supplementation by cattle grazing wheat pasture have been mixed. Anderson et al. (1987) observed that daily gains of stocker steers (246 kg) were greater when calves were supplemented with a high UIP source (1.03 kg/d) than when they received an energy supplement (0.91 kg/d). Similarly, McCann et al. (1991) observed trends for linear increases in daily gains when steers grazing high-quality wheat-annual ryegrass pastures were supplemented with 120 and 250 g/d UIP (control steers gained 1.47 kg/d vs 1.61 kg/d for the higher UIP level). However, the advantage in gain for UIP-supplemented steers was lost when cattle subsequently were finished on a common diet. Work by Donaldson et al. (1991) would suggest that much of the improvement in gain observed by McCann et al. (1991) was due to increases in forage intake when the UIP was supplemented. In their digestion study, forage intake increased from 7.3 to 10.4 kg/d when UIP was supplemented. In contrast to the above studies, neither Horn et al. (1989) nor Smith et al. (1990) observed any benefit of providing protein rather than energy supplements to steers and heifers grazing wheat pasture.

The conclusion derived from the above studies with cattle grazing grass or fed grass hays is that increases in UIP supply can improve performance slightly. However, it is unlikely that these differences would be of economic benefit, particularly if ownership of the cattle does not change between the growing period and the subsequent finishing period where the advantage to supplementation may be lost.

In contrast to the situation for grazing cattle or those fed hay, cattle fed grass silage respond to supplementation with UIP with relatively large improvements in

gains. Veira et al. (1985, 1988, 1990, 1995), Petit and Flipot (1992), Sanderson et al. (1992), and Nelson (1997) all observed improvements in performance when growing cattle fed grass silages were supplemented with fish meal or other UIP sources with the improvements ranging from 0.2 to 0.45 kg/d. Silage intakes (% of BW) were not impacted by supplementation, and responses to UIP supplementation were observed across different qualities of silage (based on performance of cattle fed only silage) and across different levels of intake. Sanderson et al. (1992) demonstrated linear responses to fishmeal supplementation for lightweight (110 kg) steers fed silage ad libitum or restricted to 1.6, 1.9, or 2.2% of BW. Petit and Flipot (1992) demonstrated in a single study that responses to fishmeal supplementation were greater when timothy silage (19.3% CP) rather than timothy hay (14.1% CP) was fed. In contrast, Seoane et al. (1993) did not observe a significantly greater response to fishmeal supplementation when grass silage rather than grass hay was fed. In that study, much of the advantage to UIP supplementation was lost during a subsequent grazing period.

Relatively large improvements in gain in response to UIP supplementation would suggest that the UIP supplement corrected an AA deficiency and increased protein deposition in those cattle. Grass silages generally contain high levels of CP, but much of this protein is either nonprotein N or is extensively degraded during the silage fermentation. Thus, the UIP content of grass silages is usually quite low. Additionally, the energy available for fermentation by ruminal microbes is low in silages due to its utilization by microbes during the silage fermentation; this leads to lower amounts of microbial protein production in the rumen when cattle are fed silages rather than hay. These factors taken together account for the greater energy to metabolizable protein ratios supplied by silages and, thus, the greater ability of cattle fed silages to respond to UIP supplementation.

Implications

Amino acid requirements of grazing cattle scarcely have been studied. Results from studies that have evaluated supplementation of ruminally undegraded protein to grazing cattle can be used to predict situations in which basal supplies of amino acids are limiting. Responses to ruminally undegraded protein in forage-fed cattle are generally small if ruminally degradable protein needs have been met; this can be attributed to the relationships between dietary energy supply, amino acid supply, and amino acid requirements. Protein deposition, which impacts amino acid requirements, and ruminal synthesis of microbial protein, which impacts amino acid supply, are both energy-dependent processes. Thus, under normal feeding conditions, deficiencies of amino acids are unlikely to be severe. Diets based on grass silages are likely to provide inadequate supplies of amino acids for growing cattle due to low

microbial protein production and low ruminally undegraded protein content in the silages.

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