Importance of Nitrogen Recycling to Beef Cattle Grazing Low-Protein Forages

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Introduction

To maximize digestion by cattle, ruminal microbes require adequate nourishment. For cattle consuming poor-quality forages, nitrogen (N) is the nutrient that is typically most limiting for the microbes (Köster et al., 1996). The total amount of N required by the microbes would minimally be the amount of microbial N flowing from the rumen and to the small intestine, but an additional amount of N equal to that lost from the rumen as ammonia would also be needed. Level 1 of the NRC (1996) model sets the microbial requirement for degradable intake protein (DIP) as 13% of TDN intake, which would be the predicted amount of microbial crude protein (MCP) leaving the rumen.

Nitrogen can be provided to ruminal microbes from DIP consumed as part of the diet, from urea recycled to the rumen across the ruminal epithelium or through saliva, and from endogenous secretions (besides urea) that contain N. Level 1 of the NRC (1996) model ignores recycled N as a source of ruminally available N (RAN) for the microbes; this is conceptually flawed but nonetheless useful in its simplicity because ruminal losses of ammonia may be balanced fairly closely by endogenous inputs of N when dietary N supplies are near the requirement for meeting microbial needs.

Total flows of N to the duodenum of cattle fed poor-quality (low-protein) forages exceed N intakes, demonstrating that urea recycling and other endogenous secretions of N play an important role in ruminal N metabolism. For example, Lintzenich et al. (1995) reported that microbial N flows of cattle fed prairie hay were about twice the predicted intake of DIP, with much of the N used by the microbes likely being provided from recycled urea. Similar observations were made by Wickersham et al. (2008a, 2009).

Urea recycling in cattle fed low-quality forage

In general, the percentage of dietary N that is recycled to the gut declines as dietary N intake increases, but the total amount of urea recycled to the rumen increases (NRC, 1985). For cattle fed prairie hay (approximately 5% crude protein) without supplemental protein, more than 95% of the body's urea production was recycled to the gut (Wickersham et al., 2008a, 2008b). Thus, cattle that are strikingly protein-deficient

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are quite efficient in moving urea to the gut, and there is little room for improving the efficiency of recycling. Due to the high efficiency of urea recycling by cattle fed low-protein diets, the total amount of urea recycled to the gut is essentially proportional to hepatic urea production when protein supplies are grossly inadequate. Any urea not recycled to the gut is lost by urinary excretion of urea.

Utilization of recycled urea by ruminal microbes

There are several potential inefficiencies in the utilization of recycled urea-N by cattle. One issue is that urea recycled to the gut may enter the rumen or post-ruminal segments of the gut (i.e., the intestines). However, urea-N entering the rumen would be the only portion that would be of significant value. This is because urea-N moved into the small or large intestines would not support microbial growth in the rumen, and as such would not support improvements either in ruminal fermentation, which could improve overall diet digestion, or in ruminal synthesis of microbial protein, which would provide metabolizable protein to the animal. Movement of urea to the intestines is largely controlled by plasma urea-N (PUN) concentrations. Under conditions of protein deficiency, which result in low PUN, post-ruminal recycling of urea-N is minimal. In contrast, for cattle fed diets containing adequate or surfeit amounts of protein, recycling of urea to the post-ruminal gut could become significant.

Urea that is recycled to the rumen is hydrolyzed to ammonia, which subsequently may be utilized by the ruminal microbes or reabsorbed across the rumen wall. In the latter case, ammonia would largely be extracted from portal blood by the liver with subsequent re-synthesis of urea. This cycling of urea-N to the rumen and ammonia-N to the liver would have a small metabolic cost for the animal, but it may be of value in providing a somewhat continuous source of N to ruminal microbes under conditions where dietary protein inputs are intermittent.

As supplementation with DIP increases, more ammonia-N derived from its ruminal degradation is absorbed (lost) from the rumen. Similarly, more ammonia-N derived from recycled urea was lost from the rumen as supplementation with DIP increased (Wickersham et al., 2008a). Consequently, the proportion of recycled urea-N that is captured by ruminal microbes should decrease with increased protein intake as a consequence of greater ammonia losses from the rumen.

Ammonia that is derived from recycled urea and lost from the rumen largely appears as urea-N returned to the ornithine cycle (ROC; Lobley et al., 2000). Indeed, protein supplementation increases total urea synthesis, total urea recycling, and ROC (Wickersham et al., 2008a, 2008b, 2009). Because ROC increases with dietary protein intake, it would be expected that a lesser percentage of recycled urea-N would be captured by the ruminal microbes when N supplementation is provided.

Both Wickersham et al. (2008b) and Bailey (2010) observed a lesser proportion of recycled urea being captured by ruminal microbes as protein supplementation increased, but in several studies (Wickersham et al., 2008a, 2009), this proportion was

not impacted by protein supplementation. Differences among studies may relate to the impact of treatments on amounts of microbial protein synthesis.

Microbial incorporation of recycled urea-N

For unsupplemented cattle fed low-quality prairie hay, recycled urea provided about one-third of the N present in bacterial protein leaving the rumen (Wickersham et al., 2008a, 2009). The proportion of microbial N that is derived from recycled urea is impacted by supplementation and can vary depending upon the frequency as well as the type and amount of supplemental N provided to cattle.

When cattle fed prairie hay were supplemented with DIP, forage intake, ruminal digestion, MCP production, urea recycling to the gut, and microbial utilization of the recycled urea-N increased (Wickersham et al., 2008a). In addition, recycling accounted for a numerically lower proportion of MCP production as DIP supplementation increased; this relationship was observed because N available to rumen microbes from urea recycling increased in amounts equal to about two-thirds of the supplemental N intake.

In cases where a protein supplement is provided predominantly as undegraded intake protein (UIP), recycling would be expected to be more critical than when it is provided predominantly as DIP. This is because N from DIP is directly available to ruminal microbes. In contrast, N from UIP must first be absorbed from the intestine before it is available, because amino acids must be catabolized and the amino acid-N used for urea production before being recycled to the rumen. Wickersham et al. (2009) clearly demonstrated that UIP supplementation increased urea recycling in cattle fed prairie hay, and UIP supplementation also increased the proportion of MCP that was derived from recycled urea-N. In this case, N available to the ruminal microbes from recycled urea increased, whereas the amount of N available to the ruminal microbes directly from UIP remained zero (by definition). This work demonstrated the expected result that urea recycling is more critical in situations where supplemental protein is provided as UIP than when it is provided as DIP.

Intuitively, it would seem that DIP supplementation would be more valuable to cattle than UIP supplementation when RAN most limits digestion. The N in DIP is directly available to the ruminal microbes and can also increase urea recycling, whereas N in UIP can only provide RAN through urea recycling. Indeed, if RAN provided from a supplement is calculated as DIP plus recycled urea, DIP supplementation in the study of Wickersham et al. (2008a) provided about 1.66 x DIP-N supply as RAN; this reflects that the increases in recycled urea-N were 66% of the supplemental DIP-N (Figure 1). In contrast, UIP supplementation in the study of Wickersham et al. (2009) provided about 0.98 x UIP-N supply as RAN; this reflects that the increases in recycled urea-N were 98% of the supplemental UIP-N (Figure 1). Thus, DIP provided more total RAN than UIP.

Somewhat surprising, recycled urea-N from DIP and UIP supplements was captured by the ruminal microbes with similar efficiencies (56% for DIP and 53% for UIP; Wickersham et al., 2008a, 2009). This likely reflects the timing of the delivery of the RAN, because the recycled urea-N from DIP and UIP may both have been delivered to the rumen at times when a deficiency in RAN existed (i.e., at times moderately distant from supplementation). For the DIP supplement, it is likely that a significant fraction of the RAN from DIP was lost from the rumen at times close to supplementation when ruminal ammonia concentrations were elevated.

Frequency of N supplementation

Supplementation frequency impacts the importance of urea recycling to cattle, and the response may depend on the level of supplementation. Wickersham et al. (2008b) provided steers fed prairie hay with DIP supplements either daily or every third day, and treatments provided either 131 (low) or 400 (high) grams of crude protein per day. For the steers receiving the lower level of supplementation, the amount of urea recycled to the gut, the amount of recycled urea captured by the ruminal microbes, and the percentage of MCP derived from recycled urea were not affected by frequency of supplementation (Figures 2, 3, and 4). This probably was the result of fairly efficient capture of RAN by the ruminal microbes because the amount of N supplemented was less than the microbes requirement. With efficient N capture by the microbes, even in the face of infrequent supplementation, there was not much opportunity for the importance of recycling to be affected by supplementation frequency. In contrast, the greater amount of DIP was designed to meet the requirements of the ruminal microbes when it was supplemented daily. Thus, on days when the infrequently supplemented steers received the higher level of the DIP supplement, RAN was well in excess of microbial requirements, whereas on days when they were not supplemented RAN was deficient. For the steers receiving the greater amount of DIP, infrequent supplementation (every third day) led to much greater amounts of urea recycling (Figure 2), much greater capture of recycled urea-N by ruminal microbes (Figure 3), and a greater proportion of MCP being derived from recycled urea (Figure 4). This seems logical because steers supplemented daily were not dependent on urea recycling to meet much of the microbes N needs, whereas the infrequently supplemented animals were very dependent on recycling to provide RAN for two of three days in the supplementation cycle. With the high level of supplementation, recycled urea provided 23% of the N in MCP for steers supplemented daily, whereas it provided 42% of that for steers supplemented infrequently (Figure 4).

Effects of energy supplementation on use of recycled urea

Abdoun et al. (2010) demonstrated that urea transport across the ovine ruminal epithelium was under regulatory control by luminal pH. Urea transport was greater with luminal pH of 6.2 and 6.6 than at pH of 5.8 or 7.0. They suggested that this regulation by pH would allow urea transport (i.e., recycling) to be greater during periods of active fermentation (i.e., at moderately acidic pH) such that urea recycling would be synchronized with the need of the ruminal microbes for N.

Bailey (2010) evaluated the impact of ruminal glucose supplementation on urea recycling in steers fed prairie hay and supplemented with two amounts of DIP. Total urea recycling was not affected by the glucose supplement, which on the surface suggested that the ruminal environment may not have a large impact on urea recycling. Ruminal pH in that study needs to be put in context; control steers had ruminal pH that ranged from 6.5 to 6.8, so the environment may not have been far from that required to support optimal urea recycling. The glucose was fermented rapidly and decreased ruminal pH to 5.2 at 2 hours after supplementation, and this pH may have been below the pH optimum for urea transport. Further, ruminal pH between 10 and 22 hours after supplementation was greater for glucose-supplemented steers than for control steers, and over this time, the ruminal pH of glucose-supplemented steers (average of 7.0) may have been too high to optimize urea recycling. In addition, glucose supplementation decreased PUN, which could decrease urea recycling and may have counteracted any effects of pH regulation of the urea transporters. In that same study (Bailey, 2010), ruminal glucose supplementation led to more recycled urea-N being captured by ruminal bacteria when the higher level of DIP was supplemented. Essentially, increased availability of rapidly fermented carbohydrates led to a greater requirement for RAN, which allowed greater capture of recycled urea.

Impact of animal factors on urea recycling

Production of urea is largely a substrate-driven process. Thus, animal productivity can impact urea recycling by impacting how much N is available for urea synthesis. When cattle use more N for productive purposes (i.e., growth or lactation), less N is available for urea synthesis and therefore less urea is recycled to the gut. Bailey (2010) compared urea recycling in forage-fed steers weighing 208 and 391 kg; the larger steers were physiologically more mature and deposited less N in tissue proteins than the younger steers. The more mature cattle had greater urea synthesis and greater urea recycling than the younger cattle that deposited more tissue protein. Thus, body protein utilization impacts urea recycling.

Limits to urea recycling

Recycled urea cannot provide a limitless supply of N to the gut. Nitrogen used for urea synthesis can be derived from: 1) absorbed ammonia that was generated within the rumen from degradation of DIP or from hydrolysis of recycled urea, 2) intestinally absorbed UIP, 3) intestinally absorbed MCP, or 4) body tissue (protein) mobilization. Although body protein mobilization may provide N to support ruminal fermentation, particularly when dietary N intake is low, this is not an approach that serves the animal well over an extended period of time. In addition, a significant portion of MCP is unavoidably lost in feces as undigested protein (approximately 20% of the true protein in microbes; NRC, 1996) and an additional fraction is excreted in urine as derivatives of purine catabolism (Chen et al., 1992). In the case of very-low-protein forages, the predominant source of N to support these losses would be mobilized body proteins with the N transported to the rumen as urea. Thus, cattle might experience greater body protein losses as they consume more of a very-low-protein forage; as such, they may

respond to very-low-protein forages by reducing forage intake to minimize these body protein losses.

Future opportunities

There are some practical limitations to improving the utilization of recycled urea by cattle fed low-protein forages. The amount of urea recycled is lowest when N intake is low, so on the surface it might make sense to try to increase the amount recycled. However, the proportion of urea synthesis that is recycled by cattle fed low-protein forage is quite high. In the studies of Wickersham et al. (2008a, 2009), more than 95% of synthesized urea was recycled in unsupplemented cattle, and the fraction recycled did not drop below 89% when cattle received DIP or UIP supplementation in amounts near their requirement for maximal intake and digestion of the forage. Thus, there is little room for improvement in recycling of urea to the gut of cattle fed low-protein forages.

Because nearly all of the synthesized urea is recycled in cattle fed low-protein forage, one might consider ways to increase urea synthesis. This process, however, is essentially limited by available N, and beyond dietary supplementation the only option for making more N available for urea synthesis would be body protein mobilization, which would be detrimental to the animal over the long term.

It does appear that there may be inefficiencies in the capture of recycled urea-N by ruminal microbes. Across the studies of Wickersham et al. (2008a, 2008b, 2009), ruminal microbial capture of recycled urea-N ranged from 45 to 72%. Some of the inefficiency may reflect recycling of urea to the intestines rather than to the rumen, but a greater portion of the inefficiency is probably related to absorption (loss) of ammonia (from urea hydrolysis) across the rumen wall. It may be possible to limit ammonia absorption by supplementing with rapidly fermentable carbohydrates that stimulate microbial growth and thereby decrease concentrations of ammonia in the rumen. At the same time, the absorption of ammonia across the rumen wall may not represent a true inefficiency in N capture if most of the ammonia is extracted by the liver and converted to urea, which can subsequently be recycled to the rumen. The primary expense associated with ammonia absorption would not be a loss of N from the system, but rather the small amount of energy required for the hepatic synthesis of urea from ammonia.

Clearly, the cow fed a low-protein forage is efficient in recapturing urea-N. In contrast, cattle fed greater concentrations of dietary protein are less efficient in capturing the urea via recycling, but at the same time they are less dependent upon recycled urea as a source of RAN and, as such, probably would not benefit much from more urea being recycled to the rumen.

Practical aspects

With increasing costs of labor and fuel, infrequent supplementation of grazing cattle has become more popular. The ability of cattle to recycle urea-N to the rumen clearly plays an important role in the success of this management technique. Infrequent supplementation of cattle has been implemented without much consideration of the impacts of recycling, but with improvements in our knowledge in coming years we may be able to better predict how cattle will respond to different amounts and types (i.e., DIP and UIP) of protein supplemented at various intervals.

Because cattle fed low-protein forages are efficient in recycling urea to the rumen, there is probably not a lot of opportunity to modify animal physiology to strikingly improve the efficiency of recycling. We can, however, use our knowledge about urea recycling to more effectively formulate supplements for cattle. One way to use knowledge about urea recycling would be in calculating the amount of RAN provided by diets and comparing this to the microbial requirement. This should improve precision of diet formulation by better matching N supply with N requirement. The key factor beyond dietary protein content that impacts the amount of RAN provided to cattle is the proportion of DIP and UIP comprising the protein consumed. As discussed above, DIP is more efficacious in providing RAN than is UIP.

Energy supplementation is a factor that might impact the capture of recycled urea by ruminal microbes. Supplementation of rapidly fermentable feeds, such as sugars, can stimulate microbial growth and increase microbial utilization of recycled urea.

Conclusions

Cattle can be quite efficient in recycling urea-N to the rumen to support the needs of the ruminal microbes. The processes of urea recycling are moderately well understood today, but further quantitative data will be required before we can fully incorporate urea recycling into models to accurately predict effects of dietary, animal, and management factors on RAN.

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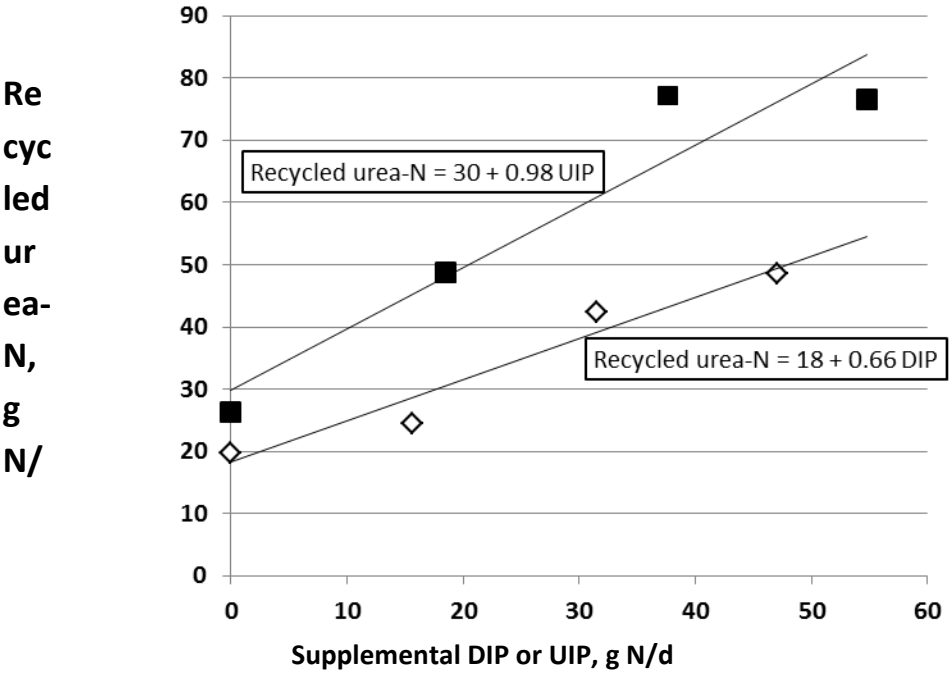

Figure 1. Effect of supplementation with DIP (open diamonds, data from Wickersham et al., 2008a) or with UIP (shaded squares, data from Wickersham et al., 2009) on urea recycling (gut entry rate) in cattle fed prairie hay.

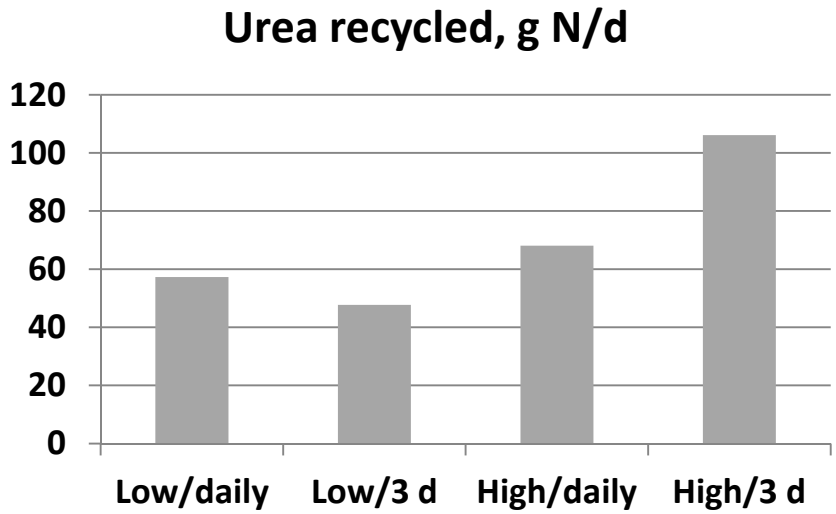

Figure 2. Impact of low (limiting) or high (adequate) amounts of DIP supplemented daily or every third day (3 d) on urea recycling in steers fed prairie hay. Within each amount, cattle received the same amount of supplement over the 3-day period. Data is from Wickersham et al. (2008b). When evaluated within the low supplementation level, frequency of supplementation did not affect (P = 0.59) urea recycling. When evaluated within the high supplementation level, infrequent supplementation tended (P = 0.07) to increase urea recycling.

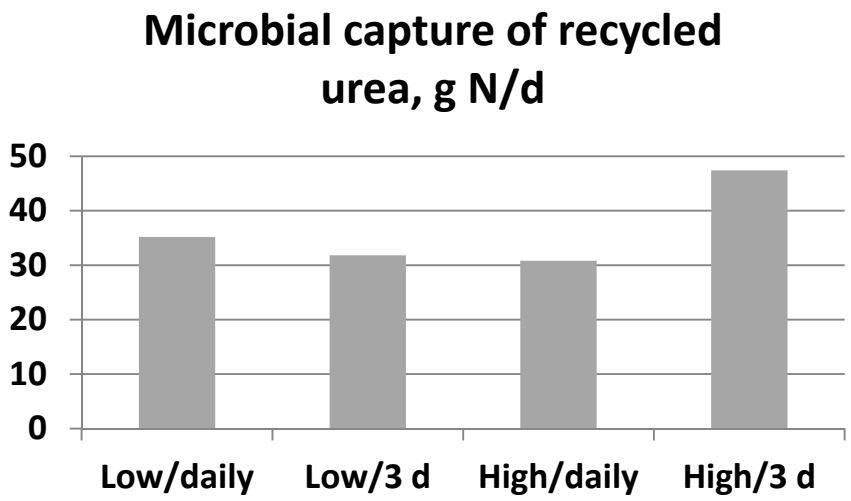

Figure 3. Impact of low (limiting) or high (adequate) amounts of DIP supplemented daily or every third day (3 d) on microbial capture of recycled urea-N in steers fed prairie hay. Within each amount, cattle received the same amount of supplement over the 3-day period. Data is from Wickersham et al. (2008b). When evaluated within the low supplementation level, frequency of supplementation did not affect (P = 0.90) microbial capture of recycled urea-N. When evaluated within the high supplementation level, infrequent supplementation increased (P = 0.03) microbial capture of recycled urea-N.

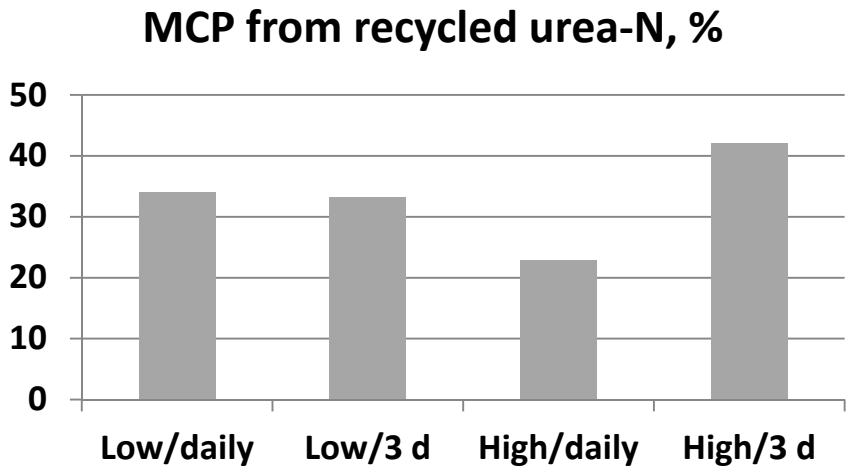

Figure 4. Impact of low (limiting) or high (adequate) amounts of DIP supplemented daily or every third day (3 d) on the percentage of MCP derived from recycled urea-N in steers fed prairie hay. Within each amount, cattle received the same amount of supplement over the 3-day period. Data is from Wickersham et al. (2008b). When evaluated within the low supplementation level, frequency of supplementation did not affect (P = 0.90) the percentage of MCP derived from recycled urea-N. When evaluated within the high supplementation level, infrequent supplementation increased (P = 0.03) the percentage of MCP derived from recycled urea-N.

SESSION NOTES