Improving protein utilization in silage to increase animal performance and reduce environmental burden

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ABSTRACT: Silage normally contains between 12 and 22 % crude protein (**CP**). While such levels should be adequate for most productive livestock, in silages they are not. This is because of poor utilization of N in silage. Most silage-based production rations require supplemental protein to meet requirements for growth or lactation in ruminants. Silage protein is highly degradable in the rumen and as such is a poor supply of dietary protein and peptides to the small intestine. The situation is exacerbated by a scarcity of available energy in the rumen which limits microbial protein synthesis. Associated with poor utilization of silage N by ruminants are concomitant high losses of silage N to the environment. Poor utilization of silage N by ruminants is attributed to proteolytic activity by crop enzymes shortly after harvest and further microbial breakdown of protein during ensilage. The production of low molecular weight nitrogenous compounds, including ammonia, amines and amides, has a negative effect on voluntary intake of silages. This appears to relate to an ammonia burden in the blood stream as well as specific appetite suppressing characteristics of certain compounds. The poor utilization of silage N in combination with lower voluntary intake of silages can seriously limit ruminant production. Methods to improve silage protein utilization exist, including improved crop drying rates, use of microbial and chemical additives and use of, or selection for, crops having characteristics that reduce protein solubility. In future, the emphasis will move away from additives and towards plant breeding and management practices.

Key Words: Protein utilization, Proteolysis, Ruminal fermentation, Silage, Voluntary intake

Introduction

Conserved forages represent a major portion of ruminant diets and ensiling offers an effective method of preservation. It is less weather dependent than hay, is readily mechanized and lends itself to large-scale production practices. However, ensiling alters the nutritional characteristics of forage. Research conducted in the 1970's and 80's by J.W. Thomas and co-workers examined many of the fundamental processes involved and paved the way for later research aimed at minimizing the effects of ensiling on forage utilization (Thomas, 1978). Changes resulting from plant enzyme and microbial activity reduce the feeding value of forage. Non-structural carbohydrate is oxidized or fermented to organic acids. Forage protein becomes more soluble and can be catabolized to non-protein nitrogen (**NPN**). These changes can have deleterious effects on silage intake and utilization leading to reduced levels of animal production from ensiled forages. Generally the more extensive these changes, the more deleterious their effects on animal production. This review will consider the impact, causes and amelioration of protein degradation in silage. Reference will be made to the impact on the animal and the environment.

Silage Protein Characteristics and Animal Requirements

Protein in silage can be characterized as being highly soluble, rapidly degraded in the rumen and present in high concentration. Table 1 compares average protein characteristics in silage with typical crude protein “requirements” for different classes of productive livestock. It can be seen that, on the face of it, ensiled forages should be able to meet the requirements of even high producing dairy cows. This, of course, it not true in practice, because of poor utilization of silage protein. The NRC requirements for beef and dairy cattle (NRC, 1996; NRC, 2001) show all-silage diets to be deficient or only just adequate in their supply of metabolizable protein (**MP**) for average levels of production. This implies wastage of excessive crude protein (**CP**) and losses of N to the environment which has implications for nutrient management on the farm. A substantial body of research has shown that silage-based diets need supplemental protein whether given to growing cattle (Veira et al., 1994), dairy cattle (Robinson et al., 1992; Broderick, 1995) and even beef cows (Charmley et al., 1999) This is well illustrated in the trial of Charmley et al. (1999) where lactating beef cows fed a silage containing 14 % CP were supplemented with up to 800 g d^{-1} corn gluten meal (**CGM**) from calving in January to turn-out to pasture in June. Calves exhibited a quadratic response in growth rate and this was reflected in a similar response in weaning weights in the fall (Table 2). If such a response can be found with beef cows, who have relatively low protein requirements, it is clear that similar or larger responses with other classes of livestock are to be expected.

Poor N utilization from silages is a product of two consequences of ensilage: solubilization of protein and fermentation of soluble sugars to VFA and lactic acid. Protein solubilization reduces the proportion of undegraded protein passing from the rumen to the small intestine. Energy yield and utilization from VFA and lactic acid is considerably less than from non-fermented carbohydrate, thus the efficiency of utilization of fermented organic matter for microbial protein synthesis is only approximately 60 to 70% of that for energy from non-fermented feeds (ARC 1984).

Proteolysis and Silage Protein Utilization

The major factor responsible fo increased rumen solubilization of silage protein compared to unensiled crops is plant proteolysis. Activity by plant protease enzymes is responsible for the conversion of true protein into smaller peptides and individual amino acids. This process is distinct from the catabolism of amino acids by certain micro flora in silage resulting in the production of ammonia, amides and amines (McDonald et al., 1991). The extent of proteolysis is dependent upon the crop species (Papadopoulos and McKersie, 1983) and the rate and extent of both drying (Muck, 1987) and pH decline (Charmley et al. 1994) as shown in Figure 1(Charmley and McQueen , unpublished). We employed three levels of acid treatment (0, 5 and 10 L carboxylic salts t^{-1} crop) and three wilting periods under good drying conditions (0, 24 and 48 h). The results showed that extensive wilting combined with the highest rate of additive, preserved 80 % of the original protein N present in the crop at ensiling. This compared with less than 40 % of the original protein N being preserved when no wilting or additives were employed.

Charmley and Veira, (1990a and b) used heat treatment to prevent proteolysis in alfalfa immediately after cutting and elicited a major response in protein utilization. Short duration, high temperature exposure effectively denatured plant enzyme activity without the protein binding effect often associated with heat-damaged silages (Table 3). Restriction of proteolysis reduced rumen ammonia concentration, increased flow of CP to the duodenum and this resulted in increased growth and CP retention by the animal.

Forage species has a major impact on utilization of CP in silage. Legumes typically have higher CP content than grasses, however it is possible to have high CP in grasses which allows for inter-species comparison. Charmley (2002) compared Westerwolds ryegrass with alfalfa silage. The CP content of the two silages was 22 and 20%, respectively. Growing steers were fed all-silage diets, where the alfalfa was progressively substituted with ryegrass. Both silages were similar in all respects, except that the ryegrass silage contained less soluble N and ammonia. Contrary to expectations, as alfalfa was substituted with ryegrass, intake did not decline but animal gains increased (Figure 2). This study exemplifies the overriding effect protein quality can have on silage utilization and demonstrates that protein characteristics differ among crops.

The high solubility of alfalfa protein is well recognized and combination of alfalfa with other forage species has been shown to improve utilization of CP. Dhiman and Satter (1997) fed a 50% forage diet to cows producing approximately 30 kg d^{-1} milk. The forage portion of the diet was either all alfalfa, 1/3 corn silage or 2/3 corn silage. Substituting alfalfa for corn silage reduced CP intake but increased the efficiency or protein utilization, thus reducing CP excretion to the environment by 15% (Figure 3). In a similar trial, but with late lactation dairy cows where the forage portion of the diet was 90 %, Charmley et al. (1993) also observed that substituting alfalfa with corn silage reduced CP losses to the environment. In that trial either 50 or 100% of the alfalfa/grass silage was substituted with corn silage. The optimum combination was 50/50 alfalfa/corn silage, similar to the 2/3 corn silage combination in the Dhiman and Satter (1997) study.

Considering the highly soluble nature of silage protein, it is surprising that a degradable protein source can also increase production. Robinson et al. (1992) fed high-silage (85 to 90%) diets supplemented with bloodmeal and casein in varying proportions. Casein was more effective than bloodmeal at increasing milk production and this was attributed to increased microbial protein synthesis in response to a ruminal supply of soluble peptides from casein. Other work has confirmed that peptides may be limiting in silage diets where much of the protein is in the form of amino acids (Newbold et al. 1991; Choung and Chamberlain 1993). Thus, stimulating rumen fermentation and microbial protein synthesis with degradable protein may be as effective as supplementing it with undegraded protein. In addition these two approaches can be use additively.

Rumen available energy and silage protein utilization

Combining silages of differing solubility characteristics is undoubtedly one reason why utilization can be improved by mixing silages. However, modification of rumen fermentation can also have a marked effect on CP utilization in the rumen. Energy yield and utilization from VFA and lactic acid is considerably less than from non-fermented carbohydrate (Thomas and Thomas 1985).

British rationing systems, unlike those in North America, now pay considerable attention to the fermentability of energy from ensiled diets in the rumen (AFRC, 1992). The greater the fermetability of metabolizable energy (**ME**) in the rumen, the greater is the microbial protein yield. In a survey of 93 British silage Chamberlain et al.(1993) demonstrated just how wide a range in fermentability can be expected (Table 4). The effect of this wide range in fermentable metabolizable energy (FME) on microbial protein yield and hence the need for supplementation can be large. For example, Chamberlain and Wilkinson (1996), calculated that a reduction in FME from 9 to 6 MJ kg^{-1} DM , would necessitate an additional 0.5 kg soybean meal (**SBM**) in order to maintain milk production at the same level.

Many researchers have added sugars back to silage rations in an attempt to improve protein utilization (Chamberlain et al. 1985; Charmley et al. 1991; Khalili and Huhtanen 1991). Results have been equivocal. Chamberlain et al. (1985) concluded that sucrose supplementation improved efficiency of microbial protein synthesis in limit-fed sheep. However, ruminal fermentation patterns under these conditions are characterized by extremes in rumen ammonia concentration and are not conducive to efficient ammonia capture by rumen microbes. Such conditions are not found in animals fed ad libitum (Charmley et al. 1991). Khalili and Huhtanen (1991) concluded that the beneficial effects of sucrose on the amounts of amino acids reaching the intestine was due to increased ruminal turnover rate rather than improved microbial efficiency.

Recent development in the field of plant breeding have led to the development of “high sugar” ryegrass cultivars. A recent study with growing beef cattle fed fresh ryegrass showed a marked improvement in rumen N use efficiency (Lee et al., 2002). Although CP content was not altered, rumen ammonia N was reduced and microbial N flow to the duodenum was increased (Table 5). In a similar study with dairy cattle, Miller et al., (2001) showed that the high sugar ryegrass reduced N losses in urine and increased N output in milk (Table 5).

Silage Protein Quality and Voluntary Intake

Ammonia N in silage has long been associated with reduced silage intake. In part this has arisen because it can be readily measured, and may act as a simple index of silage fermentation quality. Ammonia N in silage is predominantly a product of clostridial fermentation of amino acids. However, many of the other products of amino acid breakdown can reduce intake (Barry et al. 1978). Thus, silage ammonia concentration itself may not be important.

Ruminal ammonia levels, on the other hand, may have an impact on silage DM intake. After feeding silages, ruminal ammonia concentration can increase to 80 mg dl^{-1} (Charmley and Veira

1990a). These very high levels are not related to the level of ammonia in silage, but to the amount and solubility of CP in silage. Thus silages with a high CP content and high solubility, such as alfalfa, can result in high rumen ammonia concentration (Figure 4a). Under certain feeding situations, these conditions could lead to mild ammonia toxicosis which may reduce feed intake (Choung et al. 1990). Figure 4a shows a close relationship between the intake of non-protein N in sheep and rumen ammonia, while Figure 4b shows that as rumen ammonia increases above 25 mg dL^{-1} then Silage DM intake declines. These data would suggest that there should be a strong relationship between non-protein N in silage and silage DM intake. Analysis of published research by the author (Charmley, 2001) suggests that there is a quadratic relationship between silage protein solubility and voluntary intake and BW gain. Initially, increasing solubility leads to increases in DM intake and BW gain. However as soluble N increases above 47 % total N (when solubility is measured in tri-chloroacetic acid) then intake and gains decline markedly.

Inhibiting Proteolysis

Proteolysis is a major factor in reducing silage protein utilization and efforts to reduce proteolysis should enhance silage protein utilization. Traditional methods have centred around the reduction of proteolytic activity by either increasing crop DM or by reducing crop pH or through a combination of both. However to be effective, these methods have to have an immediate or very rapid influence on these processes.

It is known that wilting markedly reduces proteolysis by plant enzymes in the silo (Muck 1987). The faster the rate of drying, the more effective it is at reducing proteolysis (Anderson 1983). Methods to increase drying rate such as crop spreading, to expose the maximum surface area to solar radiation (Wilkinson et al. 1999), and crop conditioning to reduce plant resistance to moisture loss (Savoie et al. 1993; Frost and Binnie, 1999) should reduce proteolysis.

Crop maceration has potentially a two-fold effect; increased drying rate and more rapid pH reduction. The intense physical conditioning releases intracellular contents, thus making them available as a substrate for epiphytic lactic acid bacteria (**LAB**). Charmley et al. (1997) showed that LAB proliferation was increased, both in the field and the initial stages of ensiling (Table 6). This resulted in a more rapid reduction in pH, however there was no effect on the insoluble N fraction in the resulting silage. Work by Agbossamey et al. (1998) however did find that as extent of maceration increased, N degradability declined. These two studies differed in that Charmley et al. (1997) were unable to effect an increase in drying rate whereas Agbossamey et al (1998) were.

Acid-type additives have a similar effect on proteolysis to wilting, by inhibiting plant protease enzymes through rapid reduction in pH (Chamberlain and Quig 1987; Charmley et al. 1994). Charmley et al. (1994) demonstrated this by using three levels of acid salts on wilted alfalfa (Table 8). Results showed that proteolysis was progressively restricted as the level of additive was increased. This translated to improved growth of steers fed the same quantity of silage. Similar results have been obtained with dairy cows. For example, Nagel and Broderick (1992) increased insoluble protein in alfalfa silage with formic acid and this increased milk production by 12% (Table 8). Added acids or their salts are more effective than natural fermentation because acidification occurs within minutes of adding the additive. When relying on natural fermentation, or even inoculum-enhanced fermentation, acidification can take days or weeks.

Novel Developments to Improve Silage Protein Quality

Acceptable methods for reducing the extent of proteolysis have to be safe, simple, cost effective and reliable. None of the conventional methods available meet all these criteria. Recent plant breeding developments, however, offer the potential to meet these requirements. The breeding of high water soluble carbohydrate (**WSC**) grasses, as mentioned earlier, may lead the way to both improved silage fermentation and improved protein utilization in the rumen.

The recent understanding of the anti-proteolytic role of poly-phenol oxidase found in red clover could have wide impact. Jones et al. (1995) showed that red clover protein is hydrolysed at only 20% the rate of alfalfa protein. Breeding efforts to enhance the agronomic characteristics of red clover continue and the possibility of transferring the appropriate genes from red clover to alfalfa exists.

Within crop species there exists considerable variation in protein solubility which has not been selected for. Tamminga et al. (1991) Showed a wide variation in the degradability of ryegrass silages. The instantly soluble fraction varied between 45 and 65 % while the degradation rate varied over a 6 fold range. Tremblay et al. (2000) assessed the NPN concentration of 27 alfalfa cultivars. The NPN concentration varied from as low as 60 % to up to 71 % of total N. Similarly, in a smaller selection of bird’s foot trefoil, Papadopoulos and Charmley (unpublished) found NPN to account for between 20 to 50 % of total N. Based on these data it is reasonable to assume that a selection program for protein insolubility should produce fairly important results in reasonably short time frames.

Implications

This review contends that silage protein utilization is inefficient, which reduces the proportion of plant CP retained or excreted in milk and increases the proportion lost in urine. This highly labile

N source then becomes an environmental burden. Throughout the World legislation and guidelines are being adopted by jurisdictions that will lead to the development of ruminant production systems which are more efficient in terms of N utilization. Since the basic principles of poor silage N utilization are understood, it is incumbent upon the research community to develop methods that will mitigate against high N losses to the environment from silage-based diets. Conventional methods such as wilting or inoculant addition will continue to be refined, and newer methods, particularly in the area of plant breeding will become more important in the future.

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Table 1. Crude protein concentration of some forage crops (TDN = 65%) relative to requirements for typical production levels by certain livestock classes

	Crude protein, % DM
Silage characteristics	
Corn	9
Grasses	16
Legumes	20
Animal requirements	
Beef cow	10
Growing steer	14
Dairy cow	18

Table 2. Response by beef calves to protein supplementation of the cows' silage [a]

	Corn gluten meal supplementation, g d^{-1}					Significance of quadratic response
	0	200	400	600	800	
Cow DM intake, % BW	2.13	1.98	2.00	2.04	2.07	0.24
Calf BW gain during supplementation period, kg d^{-1}	0.78	0.83	0.91	0.86	0.76	0.03
Calf weaning weight, kg	248	264	284	265	240	<0.01

[a] After Charmley et al. (1999)

Table 3. Effect of inactivating plant enzyme activity using heat on protein solubility, CP flow to the duodenum and performance of growing lambs

	Treatment	
	Control	Heat-treated
Protease activity of forage, units $g^{-1}h^{-1}$	1.23	0.42
Insoluble crude protein, % CP	33	61
Digestion study[a]		
CP intake, g d^{-1}	215	201
CP flow to duodenum, g d^{-1}	151	182
CP lost across rumen, g d^{-1}	64	19
Growth study[b]		
DM intake, g kg^{-1} BW	28	37
Carcass gain, g d^{-1}	3	40
CP gain, g d^{-1}	0.4	17

[a] After Charmley and Veira (1990a)

[b] After Charmley and Veira (1990b)

Table 4. Fermentable metabolizable energy (FME) in 93 British silages

	Mean	Range
Dry matter, %	24	14 - 41
Fermentation acids, % DM	10	Trace - 22
Oil, % DM	32	0.8 - 4.7
Metabolizable energy, MJ kg^{-1} DM	10.3	8.8 - 11.8
Fermentable metabolizable energy, MJ kg^{-1} DM	7.5	4.4 - 9.7
Fermentability, %	73	48 - 90

[a] After Chamberlain et al. (1993)

Table 5. The effect of feeding grasses bred for high water soluble carbohydrate content on N utilization in beef and dairy cattle

	Control	High WSC
Beef cattle [a]		
Water soluble carbohydrate, % DM	16	24
Crude protein, % DM	9.9	10.4
Rumen ammonia, mg N L^{-1}	26	14
Non ammonia N entering duodenum, g d^{-1}	98	129
Microbial N entering duodenum, g d^{-1}	80	101
Non ammonia N Apparent absorption, g d^{-1}	51	71
Dairy cattle [b]		
Water soluble carbohydrate, % DM	13	17
Crude protein, % DM	9.2	10.6
N intake, g d^{-1}	290	280
Urinary N, % intake	35	25
Fecal N, % intake	42	40
Milk N, % intake	23	30

[a] After Lee et al. (2002)

[b] After Miller et al. (2001)

Table 6. Effect of maceration on silage fermentation and N solubility

	Unwilted		Wilted		Sig. of maceration
	Control	Macerated	Control	Macerated	
Drying rate, g moisture kg^{-1} DM h^{-1}	-	-	113	153	ns
DM at ensiling, %	15.8	15.4	26.4	35.4	**
Lactic acid bacteria at ensiling, $\log_{10}$ colony forming units g^{-1} fresh crop	3.75	5.16	6.51	8.30	***
pH 2 days after ensiling	5.10	4.96	5.64	5.12	**
Insoluble N of silage , % N	67.1	68.8	65.7	71.1	ns

[a] After Charmley et al. (1997)

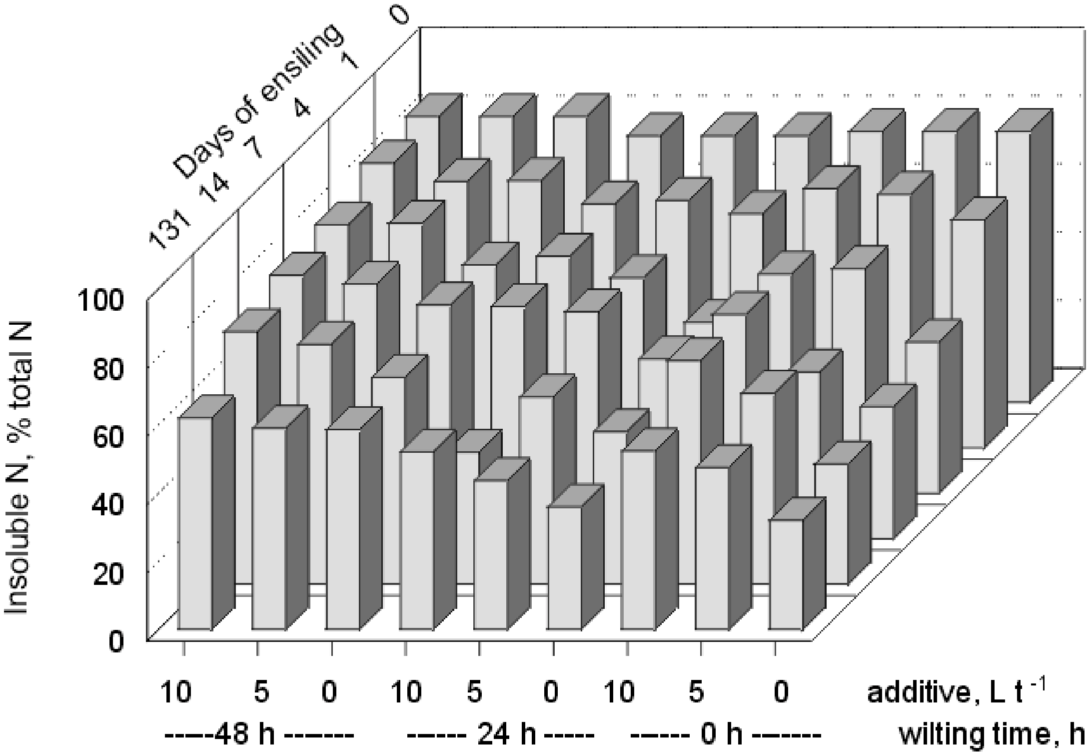
Table 7. Effect of direct acidification of silage on crop proteolysis and performance of growing steers and dairy cows fed alfalfa silage

	Additive rate [a]		
	0	4	8
Growing steers [b]			
DM at ensiling, %	34	32	34
Crude protein, % DM	18	18	18
Insoluble CP, % CP	41	55	60
DM intake, g kg^{-1} BW	31	29	30
Gain, kg d^{-1}	0.74	0.86	0.87
Dairy cows [c]			
DM at ensiling, %	38	-	35
Crude protein, % DM	21	-	21
Insoluble CP, % CP	57	-	71
DM intake, kg d^{-1}	18	-	18
Milk production, kg d^{-1}	29	-	33

[a] L carboxylic salts t^{-1} for growing steers and L formic acid t^{-1} for dairy cows

[b] After Charmley et al. (1994)

[c] After Nagel and Broderick (1992)



Charmley and McQueen (unpublished)

Figure 1. Effect of direct acidification, in combination with wilting on N solubility

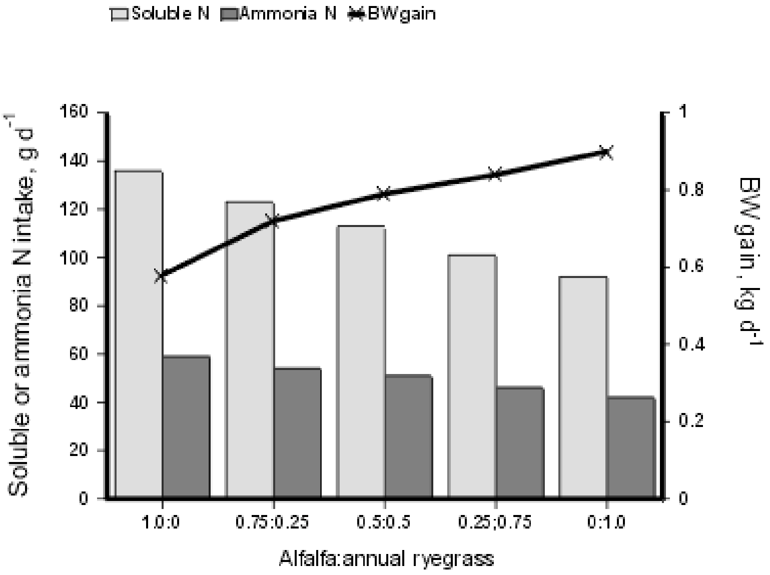
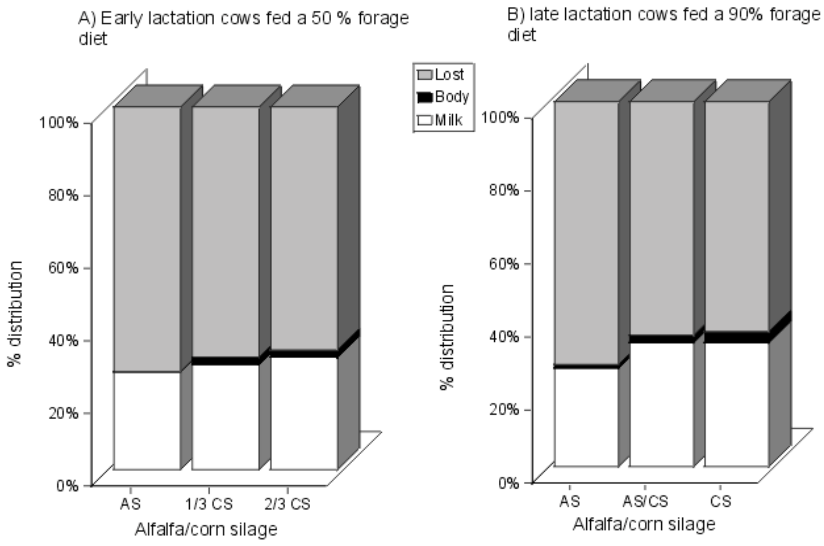


Figure 2. Effect of substituting alfalfa for ryegrass on intake of soluble of ammonia N and body weight gain in steers. After Charmley, 2002.



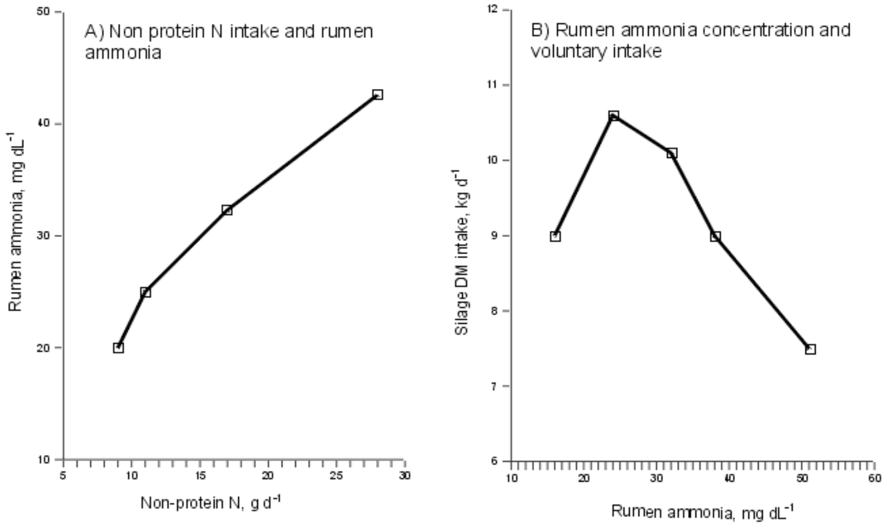
A) Early lactation cows fed a 50 % forage diet

B) late lactation cows fed a 90% forage diet

Dhiman and Satter (1997)

Charmley et al. (1993)

Figure 3. Fate of dietary protein in dairy cows fed combinations of alfalfa and corn silages.


A) Non protein N intake and rumen ammonia

B) Rumen ammonia concentration and voluntary intake

Charmley and Veira, (1990a)

Choung et al. (1990)

Figure 4. Relationship between non-protein N intake, rumen ammonia and voluntary intake of silage.