Towards improved silage quality – A review[1]

E. Charmley

Crops and Livestock Research Centre, Agriculture and Agri-Food Canada, Nappan, Nova Scotia, Canada B0L 1C0. *Contribution no. 957, received 7 July 2000, accepted 19 February 2001.*

Charmley, E. 2001. **Towards improved silage quality – A review**. Can. J. Anim. Sci. **81**: 157–168. Silage quality, as with all forages, is governed by the maturity of the crop at harvest. However, fermentation in the silo further influences nutritive value of silage by reducing voluntary intake and utilization of digestible nutrients. Silage research up to the present time has focussed on closing the gap between feeding value of the original crop and that of the resulting silage. This review focuses on the advances made towards closing that gap, and explores the possibility that in the future ensiling can become a tool for actually increasing the feeding value of forages. Following a section defining silage quality, the relationships between silage fermentation quality and voluntary intake and between silage fermentation and protein and energy utilization will be examined, with emphasis placed on measures to minimize the negative effects of fermentation on animal production. Recent literature is reviewed, which suggests that many factors previously thought to reduce silage intake, such as pH, lactic acid and dry matter (DM), have, in fact, only a casual relationship with intake. Concentrations of fermentation acids do not seem closely related to silage intake; however, they are critical in determining the balance of volatile fatty acids (VFA) produced in the rumen. This in turn, affects the non-glucogenic ratio and can influence milk and body composition in productive livestock. While rumen ammonia is often implicated in reducing silage intake, protein solubility may be more the causal agent than ammonia per se. Protein solubility is also a major factor in reducing the efficiency of silage protein utilization. Methods to reduce protein solubility in silages are discussed. Methods shown to improve silage feeding value include effective wilting and rapid acidification, either by direct acidification or the use of inoculants. Their widespread adoption has undoubtedly contributed to improvements in animal production from silages in recent years.

Key words: Silage, feeding value, voluntary food intake, fermentation, ruminant

Charmley, E. 2001. **Vers de l’ensilage de meilleure qualité – Analyse**. Can. J. Anim. Sci. **81**: 157–168. Comme c’est le cas pour les fourrages, la qualité de l’ensilage dépend du degré de maturité de la culture à la récolte. La fermentation dans le silo influe cependant aussi sur la valeur nutritive du produit en réduisant la prise alimentaire et l’assimilation des éléments nutritifs digestibles. Jusqu’à présent, les recherches sur l’ensilage avaient pour but de rétrécir l’écart entre la valeur bromatologique de la culture et celle de l’ensilage qui en dérive. L’article que voici illustre les progrès réalisés en vue de rétrécir cet écart et examine la possibilité qu’à l’avenir, on puisse se servir d’ensilage pour vraiment rehausser la valeur bromatologique des fourrages. Après avoir défini la qualité de l’ensilage, nous examinerons les relations entre la qualité de la fermentation et la prise alimentaire ainsi qu’entre la fermentation et l’assimilation des protéines et de l’énergie. Nous verrons de plus près les mesures visant à minimiser les incidences négatives de la fermentation sur les productions animales. L’article passe en revue les rapports de recherche les plus récents indiquant que maints facteurs qu’on croyait auparavant réduire la consommation d’ensilage (pH, acide lactique et matière sèche, par exemple) n’ont en réalité que des liens anodins avec la prise alimentaire. La concentration des acides de la fermentation ne semble pas non plus étroitement associée à la consommation d’ensilage. Elle joue néanmoins un rôle capital dans le bilan des acides gras volatils produits dans le rumen. Ces derniers interviennent dans le rapport non glucogénique et peuvent modifier la composition du lait et de la viande chez les bovins. Bien que l’ammoniac entrave souvent la consommation d’ensilage, la solubilité des protéines pourrait exercer plus d’influence à cet égard. La solubilité des protéines revêt aussi de l’importance dans la plus faible assimilation des protéines présentes dans l’ensilage. L’article se poursuit par un examen des méthodes permettant de diminuer la solubilité des protéines dans l’ensilage. Parmi celles qui accroissent la valeur bromatologique de l’ensilage, on retrouve un bon fanage et une acidification rapide par addition d’acide ou usage d’inoculants. L’adoption générale de ces méthodes a sans nul doute contribué à améliorer la production des animaux nourris d’ensilage ces dernières années.

Mots clés: Ensilage, valeur bromatologique, prise alimentaire, fermentation, ruminants

In most ruminant production systems, livestock derive between 40 and 90% of their feed requirements from forages. In Canada, where the winter feeding period can last for 7 mo or longer, successful forage conservation is crucial to production. Haymaking and ensiling are the only options available to farmers wanting to conserve forage on a large scale. In drier climates, haymaking is still important. However, there has been a trend over the past 30 yr or so for the proportion of forage conserved as silage to increase, while the proportion dedicated to hay has declined (Wilkinson et al. 1996).

Ensiling offers many advantages over haymaking: large quantities of forage can be conserved in a short time, forage conservation is less weather dependent and silage is well

[1]*Presented at the 2000 Forage Ruminant Workshop, Winnipeg, Manitoba.*

Abbreviations: **BW**, body weight; **CP**, crude protein; **DM**, dry matter; **VFA**, volatile fatty acids suited to mechanization. However, a major disadvantage associated with silage making is that the feeding value of the resultant forage is reduced relative to that of the original crop.

Silage research up to the present time has focussed on closing the gap between feeding value of the original crop and that of the resulting silage. Feeding value, in this case, is defined as the product of the nutritive value and potential voluntary intake of the forage (Wheeler and Corbett 1989). This review will focus on the advances made towards closing that gap and explore the possibility that in the future ensiling can become a tool for actually increasing the feeding value of forages. Following a section defining silage quality, the relationships between silage fermentation quality and voluntary intake and between silage fermentation and protein and energy utilization will be examined, with emphasis on measures to minimize the negative effects of fermentation on animal production.

DEFINING SILAGE QUALITY

For farmers, quality (or feeding value) of silage is frequently measured by a simple index, such as crude protein (CP) or total digestible nutrients. Unfortunately, these indices only reflect the growth stage at harvest and do not characterize silage fermentation. While feeding value of silage is primarily determined by digestibility, it is nonetheless influenced by silage fermentation (Steen et al. 1998). Thus, an accurate assessment of silage quality should include a comprehensive range of chemical analyses. Cost and time preclude many of these analyses on a routine basis; however, new methodologies are being developed to circumvent the need for complex analyses and yet still provide an all-encompassing measure of feeding value (intake potential, digestibility, fermentation profile). These include near infrared spectroscopy (Offer et al. 1998; Steen et al. 1998) and electromeric titration (Moisio and Heikonen 1989; Offer et al. 1998) both of which are widely used in Europe. Their adoption has been slow in North America for two main reasons. First, in North America, we are faced with a large geographical area, with diverse climatic and weather conditions, throughout which is grown a wide range of crop species. This diversification makes such methods, based on indirect relationships between feeding value and crop characteristics, unsuitable. Added to this, the North American climate is better suited to wilting than that of Europe and, in general, silage fermentation has less-negative effects on silage feeding value than in Europe. Nevertheless, ensiling does modify feeding value and, today, North American farmers are perhaps worse off than their European counterparts, because this facet of feeding value has, in large part, been ignored.

Table 1 categorises some parameters of silage quality. Routine analysis almost exclusively concentrates on factors related to the crop, and, in particular, crop maturity. Indices of silage fermentation are seldom accounted for in Canada. Furthermore, some routinely reported indices of silage quality (e.g., net energy, total digestible nutrients) are derived from acid detergent fibre or neutral detergent fibre concentration and not measured directly. Generally, producers get a reasonable assessment of crop maturity (digestibility), but a poor assessment of silage fermentation.

Table 1. Indices needed to define silage quality

Quality category	Index of quality	Routine analysis[z]
Crop related factors	Crude protein	*****
	Acid detergent fibre	***
	Neutral detergent fibre	***
	Total digestible nutrients, net energy	(*****)
Fermentation related factors	pH	**
	Protein solubility	**
	Organic acid content and profile	*
	Water soluble carbohydrate	*
	Ammonia	*

[z] ***** = almost always reported to * = almost never reported. Parentheses indicate that value is not measured directly.

Today, various ensiling techniques have evolved best suited to the size and profitability of the ruminant enterprise and the prevailing climate. Thus, round bale, bunker, bagged, heap and tower silages all have a place. Silage DM concentration can range from 20 up to 80%. Crops for ensiling range from vegetable by-products through cereals to grasses and legumes, all of which can be ensiled without or with one of several additive types. Given this diversity, it is inevitable that in many cases silage fermentation quality is critical. This becomes even more the case as ruminant rationing is refined to exactly tailor the supply of nutrients to the requirements of the animal (National Research Council 1989, 1996; Agricultural and Food Research Council 1993).

THE INFLUENCE OF SILAGE FERMENTATION ON DRY MATTER INTAKE

It is generally recognized that voluntary intake of silage is less than that of the same forage that has not undergone fermentation. This is well exemplified in Fig. 1, where the intake of silage by dairy cows declines as the concentrations of silage ammonia and butyric acid increase (Cushnahan et al. 1995). These authors achieved this relationship by ensiling the same forage for varying lengths of time (0, 21 or 63 d) before feeding to cows. Mayne and Cushnahan (1994/1995) reviewed all available literature and showed that, on average, silage intake was 27% less than intake of the same forage fed without ensiling. Today, however, we should question the validity of this conclusion. Figure 2 shows that the reduction in forage intake due to ensiling has steadily declined over the past 40 yr and recent research suggests that ensiling has relatively little impact on voluntary intake (Cushnahan and Mayne 1995; Keady and Murphy 1998). Many of the comparisons reviewed in early years were done before the widespread use of effective additives and were made on wet silages.

Fermentation Acids and Silage Intake

Butyric acid was first implicated as being responsible for reducing silage intake in 1963 (Harris and Raymond 1963). Since then other VFA have been identified (Brown and Radcliffe 1971; Wilkins et al. 1971, 1978) as well as lactic acid (Choung and Chamberlain 1993b). However, the role of lactic acid and VFA other than butyric acid in reducing

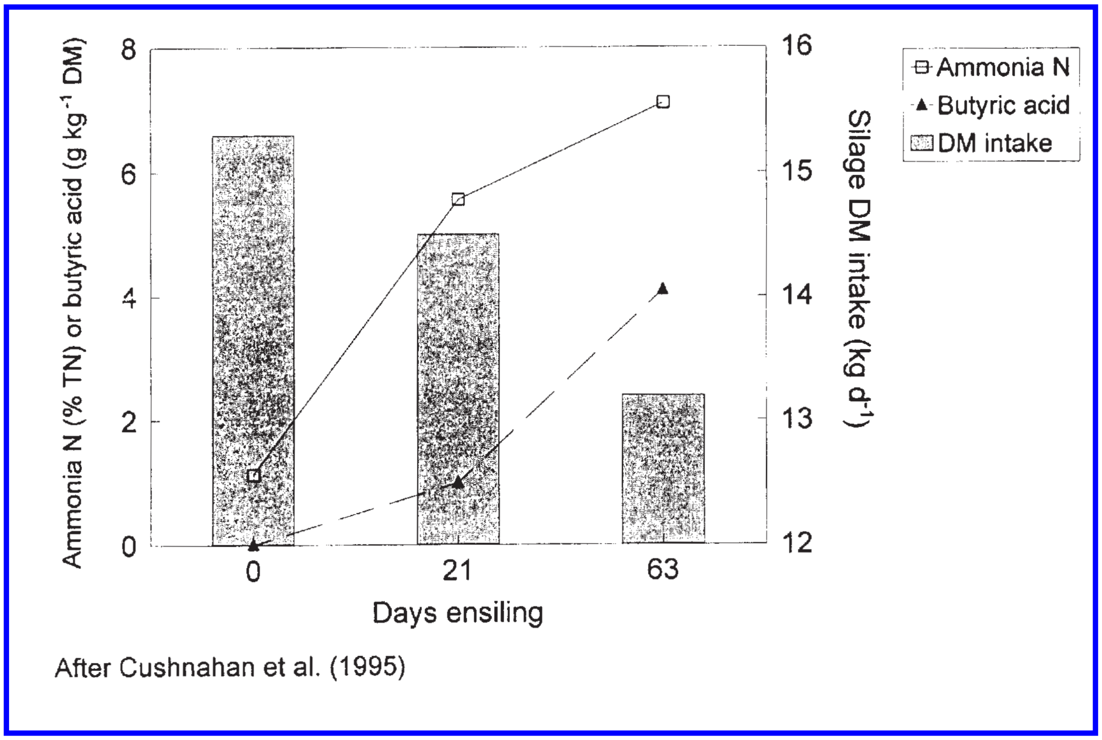

Fig. 1. Relationship between silage fermentation and voluntary intake.

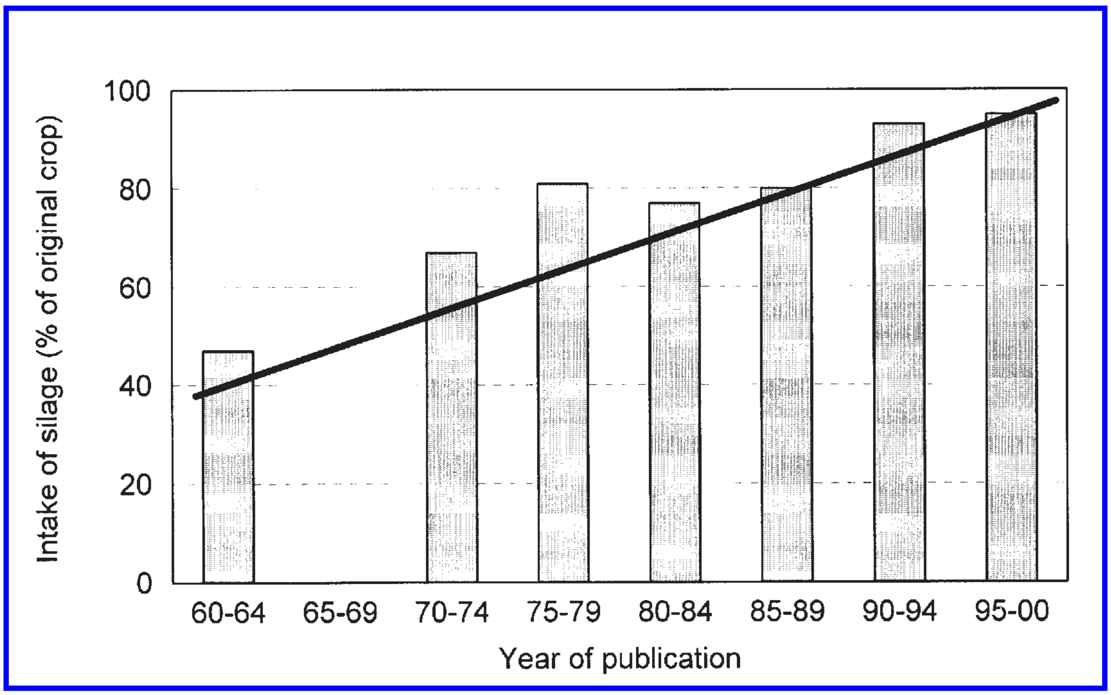

Fig. 2. Relative intake of silage compared with original crop.

silage intake remains controversial. Buchanan-Smith and Phillip (1986) infused various silage fermentation products directly into the rumen and monitored intake of a standard silage. Results were ambiguous; however, it was apparent that many silage fermentation end-products were unimportant. In a subsequent study, Buchanan-Smith (1990) assessed the effect of adding individual or combinations of VFA and ammonia on silage palatability by measuring intake for 30 min after a meal. Once again, the results were equivocal. While acetic acid did reduce intake when supplemented alone, other VFA, lactic acid and ammonia had no consistent effects. A creative approach to assessing the importance of fermentation acids on silage DM intake was adopted by Dawson and Mayne (1998). These authors squeezed juices from two silages of diverse fermentation quality and recombined these juices with the alternate silages. No relationship was found between organic acid concentration and silage DM intake.

Recently, large numbers of research trials have been reanalyzed in an attempt to predict voluntary intake from silage fermentation characteristics (Rook and Gill 1990; Rook et al. 1990; Steen et al. 1998; Wright et al. 2000). These studies found only moderate correlation between fermentation acids and voluntary intake.

Silage pH and Silage Intake

Low pH in silages is often associated with poor intakes, because low pH in the rumen reduces cellulolytic activity and depresses intake. However, there is no relationship between silage pH and rumen pH (Rooke 1995). Silage is neutralized by saliva upon consumption. Low rumen pH is typically associated with grain-based, not forage-based diets. In studies where silage intake has been increased with neutralization (McLeod et al. 1970), more recent research suggests that this is due to increased rate of passage in response to the bicarbonate (Newbold et al. 1991). Rooke (1995) and Offer (1997) have postulated that the free acid content of silage, as distinct from pH, is related to intake. However, Rooke (1995) also suggested that lactic acid may have a direct effect on palatability, because sour taste is associated with reduced palatability. Any direct effects of lactic acid on silage DM intake may be more important in the short term than the long term and related to a negative feedback (Offer 1997).

Ammonia N and Silage 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; Buchanan-Smith 1990). Thus, silage ammonia concentration itself may not be important. Nevertheless, in recent papers comparing silages of differing fermentation characteristics, ammonia still ranks as the most frequently implicated factor for reduced silage DM intake (Cushnahan and Gordon 1995; Patterson et al. 1996). A recent review by Wright et al. (2000) examined the relationship between wilting and silage DM intake. These authors concluded that ammonia concentration was correlated with the difference in intake between unwilted and wilted silages ($r^2 = 0.24$).

Studies re-analysing large data sets from European research centres have concluded that CP level (up to about 18%) and fibre were primary determinants of silage intake, but fermentation characteristics played a modifying role (Rook and Gill 1990; Rook et al. 1990; Steen et al. 1998). Broadly, this conclusion supports the original hypothesis of this review – when populations of silages are concerned, digestibility is important; however, within silages of similar digestibility, fermentation end-products have a modifying effect. Rook and Gill (1990) concluded that total VFA improved prediction, but ammonia concentration was of minor importance. On the other hand, Steen et al. (1998) concluded that ammonia was an important predictor of silage DM intake. These discrepancies probably relate to the different populations of silages used in the two assessments. Interestingly, lactic acid, pH and DM concentration in themselves were deemed not to be important determinants of silage DM intake. Early studies concluded that these were important, probably because of their close relationship with causal factors (e.g., silage of low DM content usually contains a broad spectrum of VFA).

Given the evidence presented above, it is difficult to suggest how silage intake is related to concentrations of carbohydrate fermentation end products. Despite over 40 yr of research, there is still no difinitive agreement as to which factor(s) are responsible.

Protein Solubility and Rumen Ammonia

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 (Fig. 3a). Under certain feeding situations, these conditions could lead to mild ammonia toxicosis, which may reduce feed intake (Choung et al. 1990). Figure 3a shows a close relationship between the intake of non-protein N in sheep and rumen ammonia, while Fig. 3b shows that as rumen ammonia increases above 25 mg dL^{-1} silage DM intake declines. These data 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 (Fig. 4) 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 solubility increases above 475 g kg^{-1} total N (when solubility is measured in tri-chloroacetic acid) then intake and gains decline markedly. This relationship suggests that protein solubility can be too low in silage, but is much more likely to be too high under commercial conditions, where extreme research methods to reduce protein solubility are not commonplace.

Charmley and Veira (1990a, b) used high-temperature-short term heat treatment to denature plant protease enzymes in alfalfa. This treatment dramatically reduced the solubility of CP in the silage and increased intake (Table 2). Similar responses in DM intake by reducing protein solubility have been achieved when rapid acidification (Charmley et al. 1995) or wilting (Muck 1987) was used to inhibit proteolytic activity.

THE INFLUENCE OF SILAGE FERMENTATION ON UTILIZATION OF PROTEIN AND ENERGY

Protein Utilization

Silage protein quality represents perhaps the most important determinant of silage nutritive value from an economic

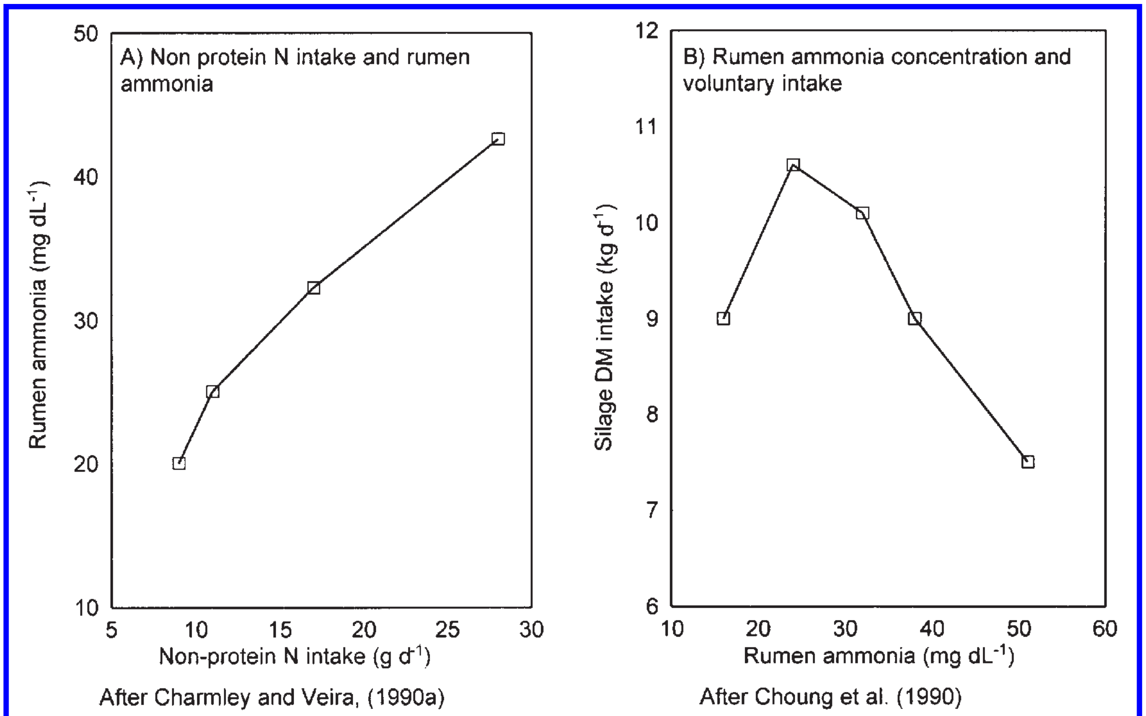

Fig. 3. Relationship between non-protein N intake, rumen ammonia and voluntary intake of silage.

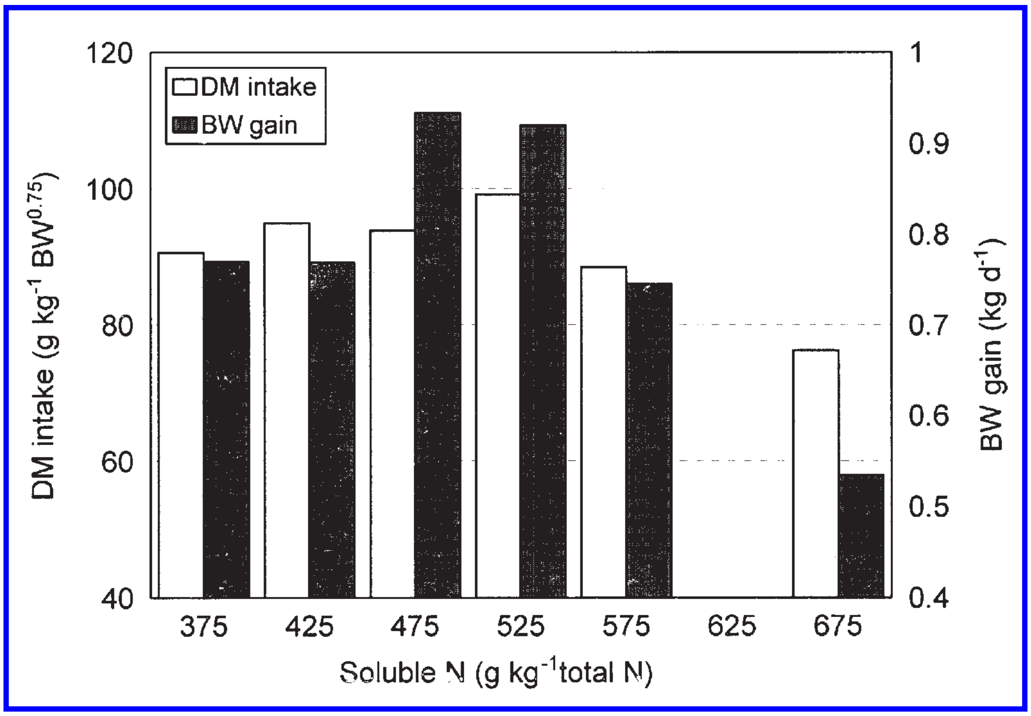

Fig. 4. Relationship between protein solubility and voluntary intake or rate of gain by silage-fed steers.

standpoint in North America. This is because most producers are ensiling crops at early maturity when digestibility is high. At this stage of growth, CP content and solubility are high (Tamminga et al. 1991; Van Vuuren et al. 1991). It is particularly an issue for alfalfa silages because alfalfa contains high levels of enzymes that solubilize protein through hydrolysis to amino acids (Papadopoulos and McKersie 1983). By comparison, red clover protein is hydrolyzed at only 20% the rate of alfalfa protein (Jones et al. 1995).

Research has shown many times that silage-based diets need supplemental protein whether given to growing cattle (Veira et al. 1985, 1990, 1994), dairy cattle (Robinson et al. 1992; Broderick 1995a) or even beef cows (Charmley et al. 1999b). This is attributed to the poor efficiency with which

Table 2. 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[z]		
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[y]		
DM intake (g kg^{-1} BW)	28	37
Carcass gain (g d^{-1})	3	40
CP gain (g d^{-1})	0.4	17

[z]From Charmley and Veira (1990a).
[y]From Charmley and Veira (1990b).

Table 3. Effect of degree of maceration on protein degradability in alfalfa silage

	Degree of maceration			
	None	Light	Moderate	Intense
Soluble	54.7	46.3	42.7	36.5
Quickly degradable	1.7	1.7	1.7	7.2
Medium degradable	31.9	36.7	38.6	40.1
Slowly degradable	4.2	7.6	8.1	6.8
Undegradeable	7.5	7.7	8.9	9.4

From Agbossamey et al. (1998).

silage protein is used in the rumen (ARC 1984). Thus, supplementation with a relatively undegraded protein source can increase production through increased undegraded intake protein supply (Broderick 1995b) and through increased silage intake (Gill et al. 1987) and digestibility (England and Gill 1985). Poor efficiency not only necessitates expensive protein supplementation, but also creates excessive excretion of surplus N into the environment (Dhiman and Satter 1997). This can be of concern in intensive ruminant livestock production areas (Tamminga et al. 1991; Broderick 1995a).

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. Energy yield and utilization from VFA and lactic acid are considerably less than from non-fermented carbohydrate (Thomas and Thomas 1985). A high proportion of VFA is absorbed directly across the rumen wall and not utilized by rumen microbes. 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 (Agricultural Research Council 1984).

Because silage fermentation depletes soluble carbohydrate concentration, 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. In support of this, Keady and Murphy (1998) found that sucrose supplementation alone did not increase intake or milk yield of dairy cows, but when sucrose plus fishmeal was fed there was a response.

In addition to poor efficiency of microbial protein synthesis, the proportion of dietary proteins escaping degradation in the rumen is also low for forages in general and silages in particular (Tamminga et al. 1991). Tamminga et al. (1991), in a survey of 35 grass silages, found that between 40 and 70% (average 61%) of CP was instantly solubilized in the rumen and only 4 to 24% was undegradable (average 9%). In comparison, for hay, only 32% was immediately solubilized with 12% undegradable. Charmley and Veira (1991) showed that the problem of high N solubility was not attributed to microbial fermentation, but to proteolysis by plant enzymes. Plant enzyme systems were inhibited by short-duration heat treatment, which reduced protein solubility, increased CP flow to the duodenum and increased CP gain in lambs (Table 2). In practical terms, plant proteolysis can be restricted by reducing pH or by increasing DM content of silage. However, to be effective, both processes have to occur within hours of cutting. Agbossamey et al. (1998) demonstrated this clearly in a trial comparing different degrees of maceration at mowing, which increases drying rate. As maceration intensity increased so did the drying rate and protein solubility (Table 3).

Charmley and McQueen (unpublished) demonstrated that both wilting and rapid acidification have an effect on protein solubility; however, these effects were only partially additive. This study 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 are summarized in Fig. 5 and 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. The potential for a combined approach to inhibiting proteolysis appears real. This would be especially beneficial if reducing protein solubility not only improves N utilization, but also increases intake of silages, as proposed earlier.

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 attrib-

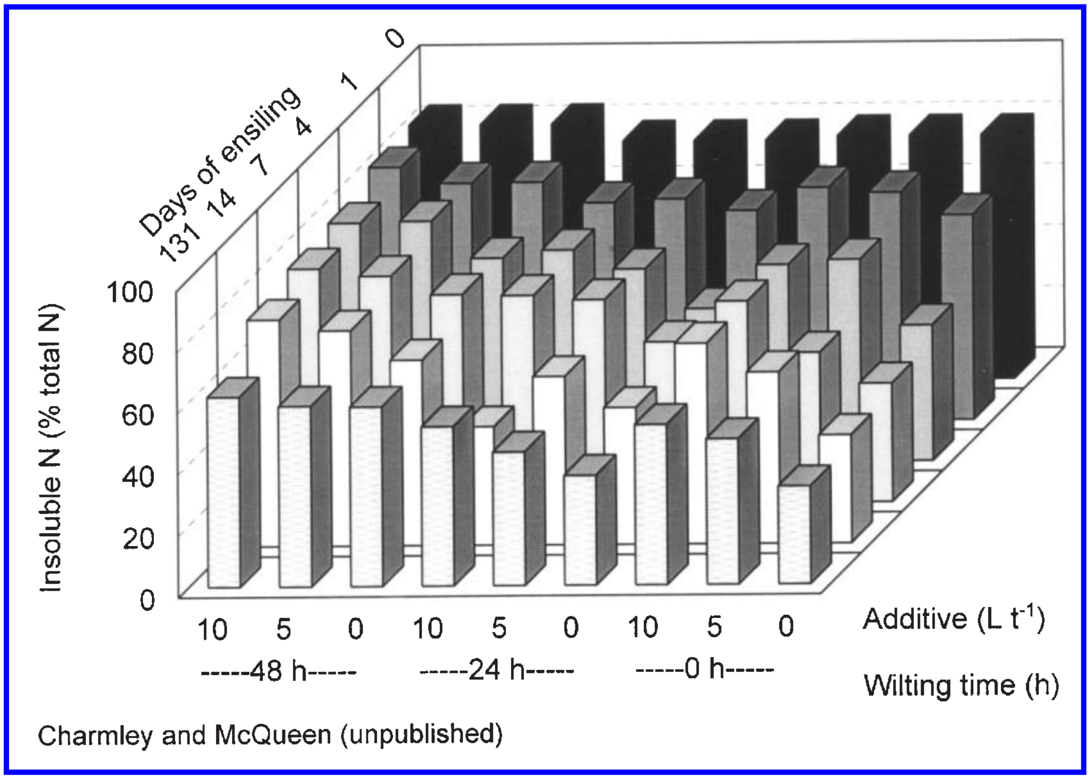

Fig. 5. Effect of direct acidification in combination with wilting on N solubility.

uted 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 1993a). 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.

Carbohydrate Utilization

Fermentation of non-structural carbohydrate in silage has a direct effect on the pattern of VFA production in the rumen. Silages that have undergone an extensive homolactic fermentation contain almost no soluble sugars; however, in excess of 10 to 15% of the DM can be as lactic acid. In addition, 3 to 6% of the DM can be as VFA. In the rumen, VFA are absorbed directly and lactic acid is metabolized primarily to propionate. This shifts the balance of fermentation end products away from lipogenic to glucogenic precursors (Jaakkola and Huhtanen 1992; Martin et al. 1994). The effect can be so marked as to reduce milk fat concentration (Cushnahan and Mayne 1995; Keady and Murphy 1996). Whereas in the past this was regarded as a problem, today it may be possible to exploit this as a tool to modify milk composition.

Relatively little attention has been drawn to the fact that ensiling can result in the conversion of structural carbohydrate to non-structural carbohydrate by plant enzymes (Heron et al. 1986). The extent of this phenomenon is clearly seen with aseptic silages (i.e., no microbial population). Charmley and Veira (1991) more than doubled initial water-soluble carbohydrate concentration in aseptic silages that had been irradiated with gamma radiation. Further, enzymic hydrolysis may be augmented by acid hydrolysis of structural carbohydrate, particularly in highly fermented silages (Heron and Owen 1991). This represents a major source of substrate for silage and possibly rumen microbes. It also explains why the energy in fermentation acids often exceeds that in the original water-soluble carbohydrate. Considering this phenomenon, it is likely that initial water-soluble carbohydrate levels are less critical than often thought to the success of fermentation. The role of direct-addition enzymes in this area is obvious; however, increased cell wall degredation in the silo is often accompanied by reduced cell wall degredation in the rumen (Sheperd et al. 1995; Nadeau et al. 1996)

MEASURES TO IMPROVE SILAGE INTAKE AND UTILIZATION

In the foregoing review, certain key elements have been shown to be critical in determining the feeding value of silage – voluntary intake, protein quality and carbohydrate fermentation. Methods of manipulating these key elements will now be considered.

Restricting Fermentation Through Wilting

There are two means of restricting fermentation; wilting and the use of acid-type additives. Wilting, to some extent, is almost universally used in North America. However, the degree of moisture loss and the wilting conditions vary, depending upon climate and prevailing weather conditions. Wilting indiscriminately reduces microbial activity in

Table 4. Effect of direct acidification of silage on crop proteolysis and performance of growing steers fed alfalfa silage

	Additive rate (L carboxylic salts t^{-1})		
	0	4	8
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

From Charmley et al. (1994).

silage, thus restricting the extent of fermentation. However, it also tends to favour lactic acid bacteria over other types, thus reducing the risk of less-useful microbial pathways dominating the ensilage process (McDonald et al. 1991). Research from the 1980s and before suggested that intake of silage was increased by wilting (e.g., Marsh 1979; Zimmer and Wilkins 1984). However, in many of those studies animal performance was not improved (Charmley and Thomas 1987) and this was attributed to reduced digestibility in wilted compared with unwilted silage, and reduced efficiency of energy utilization (Unsworth and Gordon 1985). From other work, particularly with inoculant-treated silages, this digestibility effect now seems to be due to an increase in digestibility of more extensively fermented silages rather than a reduction in digestibility due to wilting (Cushnahan and Gordon 1995). This may be attributed to hydrolysis of structural carbohydrate (Dewar et al. 1963), or modified intake and rumen outflow patterns (Thiago et al. 1992) or a combination of both. Rook and Gill (1990), in an analysis of European research, concluded the response to wilting was curvilinear with no benefits seen when DM content was above about 25%. However, in a more recent review, with a wider set of data from 79 comparisons, the response to increasing DM content in the wilted silage was linear (Wright et al. 2000). Dawson et al. (1999) showed that the greatest response to wilting was achieved under good drying conditions. Wright et al. (2000) also concluded that wilting rate, and the extent of moisture loss in wilted silages were variables most highly correlated with improved intake and performance from wilted silage relative to unwilted silages. This suggests that benefits to the animal are greatest under good wilting conditions.

It is known that wilting markedly reduces proteolysis by plant enzymes in the silo (Muck 1987, 1989). The faster the rate of drying, the more effective wilting is at reducing proteolysis (Anderson 1983). As noted previously, animal studies have linked this reduction in protein solubility to increased amino acid flow to the intestines (Charmley and Veira 1990a,b), and milk yield in lactating cows (Broderick et al. 1993). Thus, the benefits of wilting on animal performance may be related primarily to an improvement in the utilization of N by the ruminant.

Based on this review, it would appear that methods to increase drying rate will have a profound effect on animal performance. Such methods include 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). Wilkinson et al. (1999) increased drying rate by spreading swaths during wilting. Such swaths reached a higher DM concentration by ensiling. A response in intake by dairy cows was observed, but it is difficult to conclude if this was due to drying rate or the DM content at which forage was ensiled.

In studies where macerated forage has been ensiled and fed to ruminants, the effect of maceration on intake, digestibility and animal performance has been mixed. Frost et al. (1995) found that intake of ryegrass silage by sheep was reduced by maceration. However, Charmley et al. (1997) found no effect on intake or digestibility of alfalfa silage by sheep. Mertens and Koegel (1992) show that although maceration reduced silage intake in dairy cows, milk production was unaffected, suggesting better utilization of silage. Suwarno et al. (1997) observed that intake by cattle fed round bale silage was increased by maceration. Charmley et al. (1999a) found that in round bale silage there was no effect on intake, but animal gain was improved by maceration. When the same forage was fed as precision-chopped silage, intake was reduced by maceration. From these results it can be concluded that in precision-chopped silages, intake is not generally increased by maceration, and can often be decreased. Nevertheless efficiency of utilization appears to be improved. By contrast, the response is different in unchopped forage, such as round bale silage and hay (Petit et al. 1994; Savoie and Block 1994). A positive response is often observed. This suggests that maceration may mediate increased intake through a physical effect, whereas modification to chemical (fermentation) characteristics may influence efficiency of utilization. Variation in response to maceration must also reflect the variation in the degree of maceration among trials and the degree of improvement in drying rate achieved (Suwarno et al. 1999; Agbossamey et al. 2000).

Restriction of Fermentation Through Acidification

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. 1995; Keady and Murphy 1997). Charmley et al. (1994) demonstrated this by using three levels of acid salts on wilted alfalfa (Table 4). 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 5). Added acids are more effective than natural fermentation because acidification occurs within minutes of adding the additive. When relying on natural fermentation, acidification can take days or weeks.

Enhancing Silage Fermentation by Inoculation and Enzymes

Within recent years, inoculants and enzymes have become popular as a means of improving silage nutritive value.

Table 5. Effect of direct acidification of silage on crop proteoylsis and milk production in cows fed alfalfa silage

	Additive rate (L formic acid t^{-1})	
	0	8
DM at ensiling (%)	38	35
Crude protein (% DM)	21	21
Insoluble CP (% CP)	57	71
DM intake (kg d^{B1})	18	18
Milk production (kg d^{B1})	29	33

From Nagel and Broderick, (1992).

Interestingly, these work in opposite fashion to wilting in that they increase the extent of fermentation in the silo, rather than reduce it (Bolsen et al. 1992).

In a review of data up to the end of the 1980s, Spoelstra (1991) concluded that inoculation increased animal performance from silages by about 7%. Muck (1993) also reached a similar conclusion, noting a 5% improvement in milk production following inoculant use. Both reviewers concluded that a large part of the improvement in performance was due to an increase in digestibility, rather than an increase in intake. This was contrary to what was expected, since lactic acid bacteria (the principle bacterial type in inoculants) are non-cellulolytic. The increase in digestibility may be in response to the extensive fermentation of substrate to lactic acid in these silages. Under these conditions, acid hydrolysis of structural carbohydrate to soluble sugars will occur (Dewar et al. 1963). The reduction in fibre concentration has been speculated to be responsible for increases in digestibility (Heron and Owen 1991). On the other hand, Gill and Romney (1994), Thiago et al. (1992) and Teller et al. (1993) have demonstrated that highly fermented silages are eaten more slowly than less highly fermented silages or hay. If these changes in eating behaviour influence ruminal retention time, this could also explain why digestibility is increased by inoculant use.

A possible direct, probiotic effect of silage inoculation on rumen fermentation has been proposed (Gordon 1989) to explain improved animal performance from inoculated silages, in the absence of changes in silage fermentation. However, when Keady and Steen (1996) added *Lactobacillus plantarum* bacteria at 10^9 cfu g^{-1} silage at the time of feeding, they found no animal response in terms of intake, digestibility or rumen fermentation.

Evidence is increasing to suggest that lactic acid in silage favours a glucogenic balance of VFA in the rumen (Martin et al. 1994). In certain trials this has led to a reduction in milk fat percent (Cushnahan and Mayne 1995). If this proves to be a widespread phenomenon, inoculants may play a role in reducing milk fat percent.

Cellulase, hemicellulase and amylase enzymes have been widely tested as silage additives. These compounds have the potential to convert structural carbohydrate to soluble sugars, which can be fermented by silage bacteria. Many trials have shown that their use increases the level of fermentable substrate in silage, thus promoting extensive fermentation (Jaakkola et al. 1991; Jacobs and McAllan 1991; Stokes 1992). However, for most European research with relatively wet silages, there has not been an increase in digestibility, and improvements in animal performance have been generally small (Jaakkola et al. 1991; Jacobs and McAllan 1991). This may be attributed to increased effluent losses removing soluble compounds from the silage, since research with wilted silages has shown benefits in digestibility and animal performance (Fredeen et al. 1991; Stokes 1992; Fredeen and McQueen 1993). Effects on animal performance are consistent with enhanced fermentation and similar to those reported for inoculants. However, increased hydrolysis of structural carbohydrate in the silo results in reduced fermentation of structural carbohydrate in the rumen (Sheperd et al. 1995).

CONCLUSIONS

Modern ensiling technology has increased the feeding value of silages, close to that of the original unensiled forage. However, silages of poorer feeding value are still produced, and there is no consensus on what factor(s) are critical to silage feeding value. Concentrations of fermentation acids do not seem closely related to silage intake; however, they are critical in determining the balance of VFA produced in the rumen. This in turn, affects the non-glucogenic ratio and can influence milk and body composition in productive livestock. While rumen ammonia is often implicated in reducing silage intake, protein solubility may be more the cause than ammonia per se. Protein solubility is also a major factor in reducing the efficiency of silage protein utilization. Given that protein solubility is implicated in both the voluntary intake of silages and the utilization of protein in silage, it is surprising that this aspect has not received more attention, particularly in Europe. Methods shown to improve silage feeding value include effective wilting and rapid acidification, either by direct acidification or use of inoculants. Their widespread adoption has undoubtedly contributed to improvements in animal production from silages in recent years. The possibility that in future, silages will have superior feeding value to the original crop is realistic. Physical treatments can break down barriers to intake and improve digestibility. Predictable silage fermentation can be used to optimize rumen function. However, there appears to be less scope for improving on the protein quality of the original forage.

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