

CHAPTER 1

GENERAL INTRODUCTION

The Cow In Apple Time

Something inspires the only cow of late
To make no more of a wall than an open gate,
And think no more of wall-builders than fools.
Her face is flecked with pomace and she drools
A cider syrup. Having tasted fruit,
She scorns a pasture withering to the root.
She runs from tree to tree where lie and sweeten
The windfalls spiked with stubble and worm-eaten.
She leaves them bitten when she has to fly.
She bellows on a knoll against the sky.
Her udder shrivels and milk goes dry.

-Robert Frost

In the poem, *The Cow In Apple Time*, the poet Robert Frost illustrates the complexities of rumen fermentation that are influenced by dynamic interactions between the diet, microbial population, and host animal (Durand, 1989). Uncoupling of these interactions may result digestive disturbances and possibly failure of the animal to grow, lactate, or reproduce. Ruminal acidosis as poetically described by Frost, is a biochemical insult caused by the over consumption of readily fermentable carbohydrates contained in the apples (Oltjen et al., 1977; Rumsey et al., 1979; Rumsey, 1978). Shortly following consumption there is a shift in the microbial population to lactic acid forming bacteria, primary *Streptococcus bovis*. In cases of rich engorgement, *Str. bovis* continues to produce both L and D forms of lactic acid causing a precipitous decrease in rumen pH and is also absorbed into the blood. As blood pH declines so does blood pressure, causing a decline in perfusion pressure and oxygen supply to the tissues. Ultimately renal blood flow and glomerular filtration fail resulting in anuria, the animal enters shock and dies (Radostitis et al., 1994).

The balance of normal rumen fermentation is not only influenced of the supply of nutrients available for fermentation but may be influenced by the ration physical form (Mertens, 1997). More specifically, ruminants require forage fiber in coarse physical form (NRC, 2001). Increasing fiber level and forage particle size has been shown to influence chewing behavior and is believed to increase saliva flow, rumen pH, acetate-to-propionate ratio and milk fat levels (Cassida and Stokes 1986; Mertens, 2000). Although impaired rumen fermentation and function can result in cattle fed rations lacking in physical structure, excessive amounts of long, coarse forage may also limit intake and digestibility, ultimately affecting energy balance of the animal (Allen 1997).

National Research Council (2001) guidelines have proven useful in defining animal requirements and feed composition but do not provide detailed recommendation of ration physical form. Current NRC recommendations state that a minimum mean particle length of 3 mm for alfalfa diets is necessary to maintain rumen pH, chewing activity, and milk fat percentage. It is recommended that diet NDF be increased if excessively fine forages or high amounts of rapidly fermentable starch are fed. The ability to routinely measure ration particle size has been difficult

until introduction of The Penn State Particle Separator (PSPS). Using the PSPS the particle distribution of ruminant feed is determined by separating particles according to size; those > 19.0-mm, those between 19.0 and 8.0 mm and those < 8.00 mm (Lammers et al., 1996). Published studies are only beginning to report particle size distributions based on measurements of the PSPS thus making formulation of recommendations difficult.

Because chewing activity is known to be an accurate measurement of the roughage characteristics for ruminant diets, the concept of effective fiber was created to amalgamate the chemical and physical nature of the forage, and to quantify its value to rumen function (Sudweeks et al., 1981). Physically effective NDF (peNDF) is defined as that dietary fiber source which effectively stimulates rumination and salivation (Mertens 1997). Hinged to the method designed to measure peNDF is the observation of Poppi et al., (1985), who suggested that particles retained on a sieve measuring 1.18 mm pass out of the rumen slower than those not retained. Mertens (1996) proposed that in order for particles > 1.18 mm to pass out of the rumen they would have to be reduced through comminution and as a result these particles would stimulate more saliva secretion than those < 1.18 mm. As a result of this assumption, Mertens, (2000) suggested that the peNDF value of feed can be determined by measuring the amount of NDF retained on a 1.18 mm screen.

The objectives of this thesis work were to 1) further investigate use of the PSPS in measuring feed particle size and to more accurately define its operation, 2) to investigate the effects of ration particle size as measured by the PSPS on chewing activity in dairy cattle 3) and to investigate the effects of ration particle size on intake, ruminal fermentation and energy utilization of cows in early lactation.

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CHAPTER 2

LITERATURE REVIEW

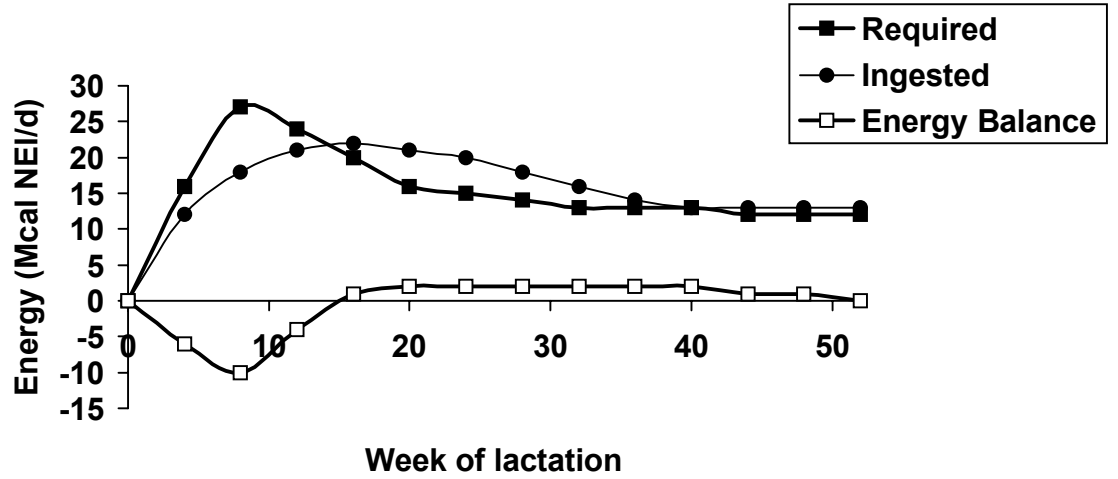
INTRODUCTION

H.P Armsby once noted that the usefulness of his work was not solely to, “enable the farmer to feed his stock more economically [but also to] elucidate knowledge of the unchanging ...chemical and physiological [laws], of nutrition (Armsby, 1880). Given our current understanding of nutrition and its complexities, we should not be surprised that during quest for establishing tables of net energy feed values, Armsby enthusiastically remarked that he saw, “in the prospect [of the net energy system] such promise that [he was] pleased to devote the rest of his life to the study of the subject (Swift, 1957). “ Since the time of his words, considerable progress has been made in the understanding of nutrient requirements and utilization in food producing animals, however our “knowledge” remains incomplete. More specifically, if we desire to more accurately understand and predict milk yield or composition, dietary nutrient supply, and intermediary metabolism of the lactating dairy cow requires further study and elucidation.

Early Lactation and Energy Balance

The onset of lactation marks a highly dynamic period of the lactation cycle. Subsequent to calving, energy intake is below that required to sustain milk secretion. During this time, demands of lactation require mobilization of nutrient body stores, most notably fat and protein (Bauman and Currie, 1980). It has been estimated that during early lactation, 40 to 90 kg of fat and 24 kg of protein may be mobilized (Komaragiri et al., 1998). Figure 2-1 illustrates that during the first third of lactation, cows are in negative energy balance (NEB) as ingested energy does not meet the energy requirements of lactation, and as a result animals must mobilize reserve. The largest change during early lactation occurs in the adipocytes. Here uptake of nutrients for storage lipids is decreased and lipid reserves are mobilized and as a result body composition changes occur (Rastani et al., 2001; Herdt, 2000). It is usually only after peak production that the cow is able to replenish reserves which will be necessary for the next lactation. After peak lactation most of the animals energy needs are met with feed intake exceeding as high as 4 % of

Figure 2-1. Energy balance of a dairy cow through one full lactation (■) required energy, (●) ingested energy, (□) overall energy balance.



live body weight (Chase, 1993), at this time body reserves are not needed to meet the needs of the mammary gland (McNamara, 1991). This physiological state of positive energy balance (PEB) usually continues until the end of lactation.

Dietary Supply of Carbohydrates During Early Lactation

Energy intake has been identified as a primary limitation of milk yield for cows in early lactation and is a function of the total amount of feed consumed and the energy concentration of the diet (Allen, 2000; Weiss 1998; Woodford and Murphy, 1988). The term nonstructural carbohydrate (NSC) collectively refers to the highly digestible sugars, starches, and reserve carbohydrates (galactans, pectin, etc.) and serves as the primary energy component in a typical dairy ration (Van Soest, 1994). Increasing energy content with the use of NSC is common practice but is usually but usually included in the ration at the expense of fiber (Varga and Kononoff, 1999). The most widely used expression of fiber content in ruminant diets is neutral detergent fiber (NDF) which is the fraction of the feed containing cellulose, hemicellulose, and lignin (Van Soest et al., 1991).

Minimum and Maximum Fiber Requirements for Dairy Cattle

Although rations high in NSC and low in NDF are high in energy, they are also more rapidly fermented resulting in a lower rumen pH, a factor which may decrease DMI, fiber digestibility, microbial yield and milk production (Allen, 1997). It has been estimated that high-energy diets result in a 40% incidence of ruminal acidosis in cows in early lactation. Additionally a number of long term effects associated with poor ruminal health may occur and may include laminitis, or displaced abomasum (Varga and Kononoff, 1999). Current nutrient recommendations (NRC, 2001) state that dairy rations should have a minimum of 25% NDF, 19% of which must come from forage for adequate rumen health (Table 2-1).

Current NRC (2001) guidelines state that maximum NDF requirements for ruminant diets are a function of the net energy of lactation (NE_L) requirements of the animal. Although rumen fermentation and function can result in cattle fed rations deficient in fiber, excessive levels of over

Table 2-1. Minimum diet and forage NDF, and maximum NFC (% DM) requirements of dairy cattle fed total mixed rations (NRC, 2001).

Minimum Forage NDF	Minimum Dietary NDF	Maximum Dietary NFC¹
19	25	44
18	27	42
17	29	40
16	31	38
15	33	36

¹ Because of the limited data available on direct non-structural carbohydrate (NSC) measurements and requirements, nonfiber carbohydrate (NFC) was calculated by difference: $100 - (\% \text{ NDF} + \% \text{ CP} + \% \text{ Fat} + \% \text{ Ash})$ (G.A. Varga, personal communication).

44% may also result in negative effects on intake and digestibility (Table 2-1) (NRC, 2001; Van Soest, 1995). Because NDF is usually correlated with energy concentration, recommendations outline that excessive levels of NDF are avoided if rations are formulated to meet NE_L requirements.

Although chemical requirement of NDF has been reasonably well defined, the source and physical nature of this component may result in interactive effects on rumen function and milk production. Because non-forage fiber sources (NFFS) possess a large proportion of NDF, small particle size and high specific gravity, rumen turnover of this component is greater than NDF of forage source and less effective in maintaining rumen pH and milk fat percentage. Current guidelines adjust recommendations for NDF based on that contributed from forage sources (Table 2-1).

The Effect of Diet Physical Form on Cows in Early Lactation

Animals in mid lactation are most often used when examining fiber requirements of dairy cattle and examining dietary effects on chewing and rumination. Okine et al., (1997) stated that the “relationships between fiber content and different NDF concentrations on chewing activity have only begun to be studied in cattle at different stages of their productive cycle.” Weigand et al., (1993) also suggested that total rumination time along with NDF level might be a limiting factor in feed intake control. It thus seems apparent that further investigation on the effects of NDF and ration particle size is required for animals in different stages of lactation, but particular, early lactation.

It is widely understood that feeding forage of short particle size effectively decreases chewing activity, saliva flow, rumen pH, acetate-to-propionate ratio and ultimately affecting milk fat levels (Cassida and Stokes 1986; Norgaard 1983). In comparison, excessive amounts of long, coarse forage may also limit intake and digestibility, ultimately affecting the energy balance of the animal (Allen 1997). Because energy requirements are highest for early lactation, and in light of the negative effects associated with fine or coarse forage, studies designed to more clearly define physical requirements and limitations of fiber are needed. More specifically, further

understanding of how ration particle size affects chewing behavior, rumen function and fermentation, intake and milk production will result in a more complete understanding of the nature of the fiber requirement and its interaction on intake and utilization of other nutrients (Woodford and Murphy, 1988; Kertz et al., 1991).

CHEWING ACTIVITIES

Introduction

Ruminants may spend 2 to 9 h/d eating and 2 to 10 h/d ruminating depending upon level of intake (Beauchemin, 1991), size of the animal (Bae et al., 1983), and the chemical as well as physical nature of the ration (Beauchemin et al., 1997, Shaver et al., 1988). Understanding of eating and rumination activities is critical in order to fully understand normal rumen function, its impact on animal metabolism, and the nutritional factors that affect it. Mammals masticate their feed to aid in the digestive process (Prinz and Lucas, 1997). In ruminants, chewing during eating and rumination functions to reduce feed particle size and to increase particle surface/volume ratio (Poppi and Norton, 1980). Alterations of the physical properties of feed results in improved microbial access, feed degradation (McAllister et al., 1994), and facilitates the passage of feed residues out of the rumen (Bernard et al., 2000; Welch, 1984). Because these alterations occur through musculature mechanisms an energetic cost is associated with chewing (Blaxter, 1989). When an animal is fed a diet composed of a poor quality roughage, up to one third of the total ME supplied in the diet may be necessary to fuel chewing activity (Susenbeth et al., 1998). Chewing also stimulates secretion of saliva, which contains high concentrations of bicarbonate and phosphate buffers and aids in maintaining a rumen pH level suitable for microbial activity (Beauchemin, 1991; Cook, 1981).

Chewing Behavior

Eating

Eating is characterized by prehension, mastication, and swallowing. Prehensive bites occur as the ruminant animal gathers feed into the mouth (Rutter et al., 1997). Using a circular

movement the animals tongue collects long or coarse particles, which are conveyed, into the mouth while smaller feed particles such as grain may also be captured and manipulated into the oral cavity by the lips (Beauchemin, 1991). Once in the mouth, masticative chews are used to grind feed into smaller particles to be swallowed. Concurrent with masticative activity, saliva is secreted and acts to cohere the boli and to facilitate swallowing and passage through the pharynx and esophagus (Murphy and Kennedy, 1993; Prinz and Lucas, 1997). Although diurnal meal patterns depend upon both the physical and chemical properties of the feed, when fed ad libitum, consumption usually occurs when feed is made accessible to the animal and then followed by a number of shorter bouts throughout the day. It has been estimated that dairy cattle may consume up to 20 meals per day depending on feed composition, availability, or requirements of the animal (Beauchemin, 1991; De Boever et al., 1990).

Rumination

The primary function of rumination is to reduce particle size thereby facilitate clearance of digest particles from the reticulorumen (Ulyatt et al., 1984). The onset of rumination is marked by the regurgitation of ingesta from the reticulorumen into the lower esophagus, and described as the “up bolus.” Immediately upon passing through the esophagus and reaching the pharynx, a small portion of liquid and fine particles is usually reswallowed (“tail bolus”). The material which remains is chewed further and then swallowed, thus named the “down bolus” (Ulyatt et al., 1984). Diurnal ruminating activity in animals raised in confinement is most often observed during the night while the animal is resting, although rumination is often observed during daylight hours. For lactating dairy cattle, approximately 10 – 20 ruminating bouts occur each day while each bout may range from one minute to over two hours in length (Beauchemin, 1991).

Measurement of Eating and Rumination Behavior

For accurate study of chewing behavior, long periods of eating and ruminating activity must be measured using electronic recordings or approximated through visual observation (Penning, 1983). Although data is reported in a similar manner using either method (i.e. min/d,

min/kg of DMI, etc.), differences between methods of measurement may exist. The IGER Behavior Recorder (Ultra Sound Advice, London, UK) is a system capable of digitally recording jaw movements of free-ranging grazing cattle (Rutter et al., 1997). Because of its compact construction and ability to function without constraint of the animal, the use of this technology provides convenient and accurate measurement of chewing activities.

The Graze software automatically identifies different jaw movements as either eating or ruminating (Figures 2-2 and 2-3) but may occasionally misinterpret the activity. This is corrected by manual review as ruminating behavior is easily identified as the regular pattern and amplitude characterized with a 5 to 10 second period between boli when no jaw movements occur (Figure 2-3) (Rutter, 2000). In comparison, the longer eating bouts are characterized with a more irregular amplitude and frequency with no inactivity associated with boli movement (Figure 2-2). Chewing activities can also be estimated concurrently through a visual observation method. Animal activity is usually observed and noted at five-minute intervals. It is then assumed that the eating, ruminating, or resting activity observed at each point in time occurred for the entire five minute preceding that observation and ended at point of the last observation. Total number of minutes eating, ruminating and resting activity is then estimated by the sum of each observation and multiplied by a factor of five (Shaver et al., 1988).

Recently Kononoff et al., (2002) compared observational and an electronic recording system and demonstrated that they agree on single bout identification of eating and ruminating activities however the electronic method was able to detect bouts less than five minutes in length thus total number of bouts was numerically higher for both eating and ruminating activities (Table 2-2). These results were slightly better than that reported by Rutter et al., (1997) who studied grazing behavior with the same technology and reported some difficulty correctly identifying chewing behavior as a result of the physical distance between the animal and the observer. On average, both total chewing time and average bout length was higher using the observational method, with the observational methods resulting in values 5% higher for eating activity and 10% higher for ruminating activity (Table 2-2). Total time ruminating was higher using the observational method in all eight observations. Total time eating was higher using the

observational method in all but two observations where differences were minimal. In summary, mean method differences for total time eating ($8.7 \text{ min} \pm 12.8$) and total time ruminating ($42.9 \text{ min} \pm 12.0$) were significant ($P \leq 0.05$). Because the observational method is a representation of activity occurring at five-minute intervals and not continuous as in the electronic measurement, differences between methods most likely indicate inaccuracies in the observational measurement and its ability to detect the exact start and finish of each chewing bout. Error most likely lies in the assumption that chewing activity occurs during the entire five minutes before the first observation and ended once the last observation was taken and that the exact start and end of each bout was not detected. Smaller discrepancy for eating activity is most likely due to the fact that it is easier to visually determine if the animal is eating as it requires more body movement than rumination, which occurs in a resting state. Observational estimation of chewing activity will most likely continue to be employed as an inexpensive but laborious method in experiments investigating effects of diet on eating and ruminating. The results of the experiment indicated that absolute values of chewing activities between experiments should not be directly compared when method of estimation is different.

Table 2-2. Number of bouts, total time (min) chewing and time per bout as well as calculated method differences as measured by the electronic system and estimated by observation (Kononoff et al., 2002).

	Observed	Electronic	Method Difference	SD	<i>P</i> - Value
Eating					
no. of bouts	9.4	9.5	0.1	0.35	0.35
total time (min)	246.9	238.1	8.7	12.8	0.09
time/bout (min)	27.9	26.0	2.6	2.61	0.08
Ruminating					
no. of bouts	14.3	14.5	0.2	0.46	0.17
total time (min)	415.0	372.1	42.9	12.0	< 0.0001
time/bout (min)	29.6	26.0	3.6	1.61	< 0.001

Figure 2-2. An example of the Graze window and recorded eating movements resulting in wave like patterns.

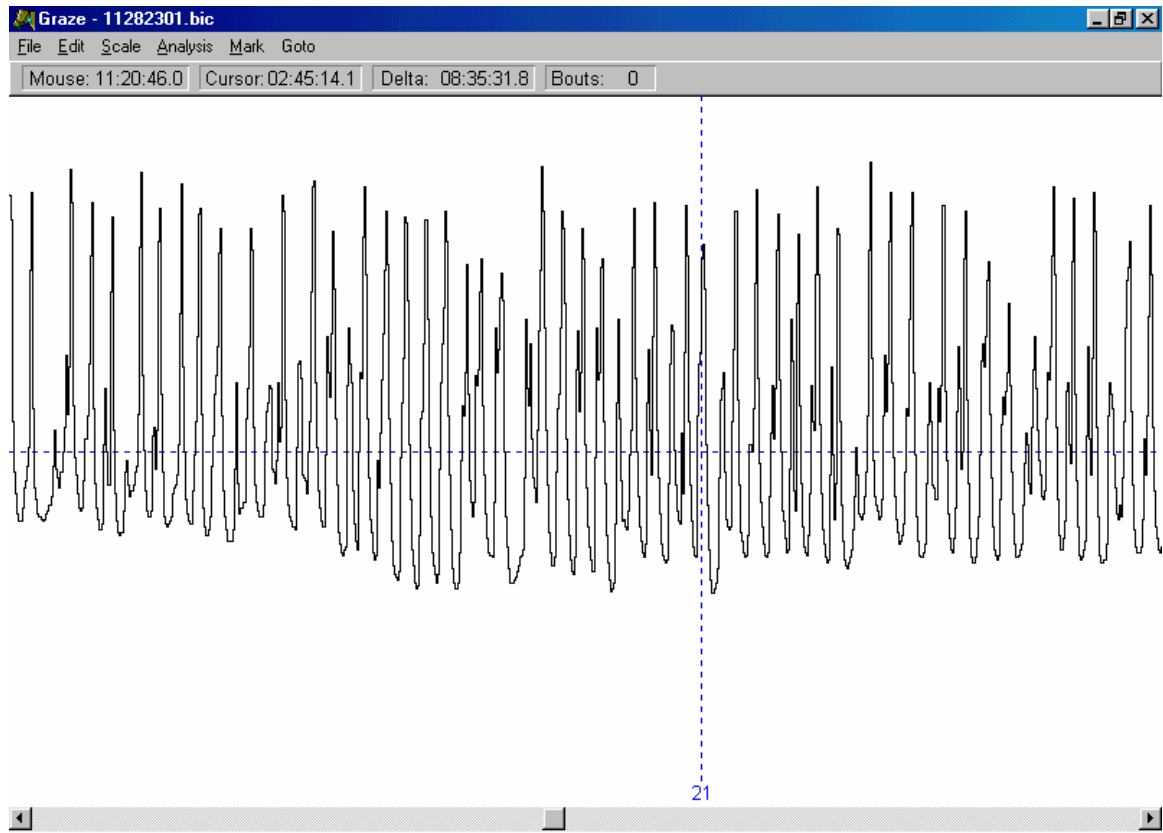
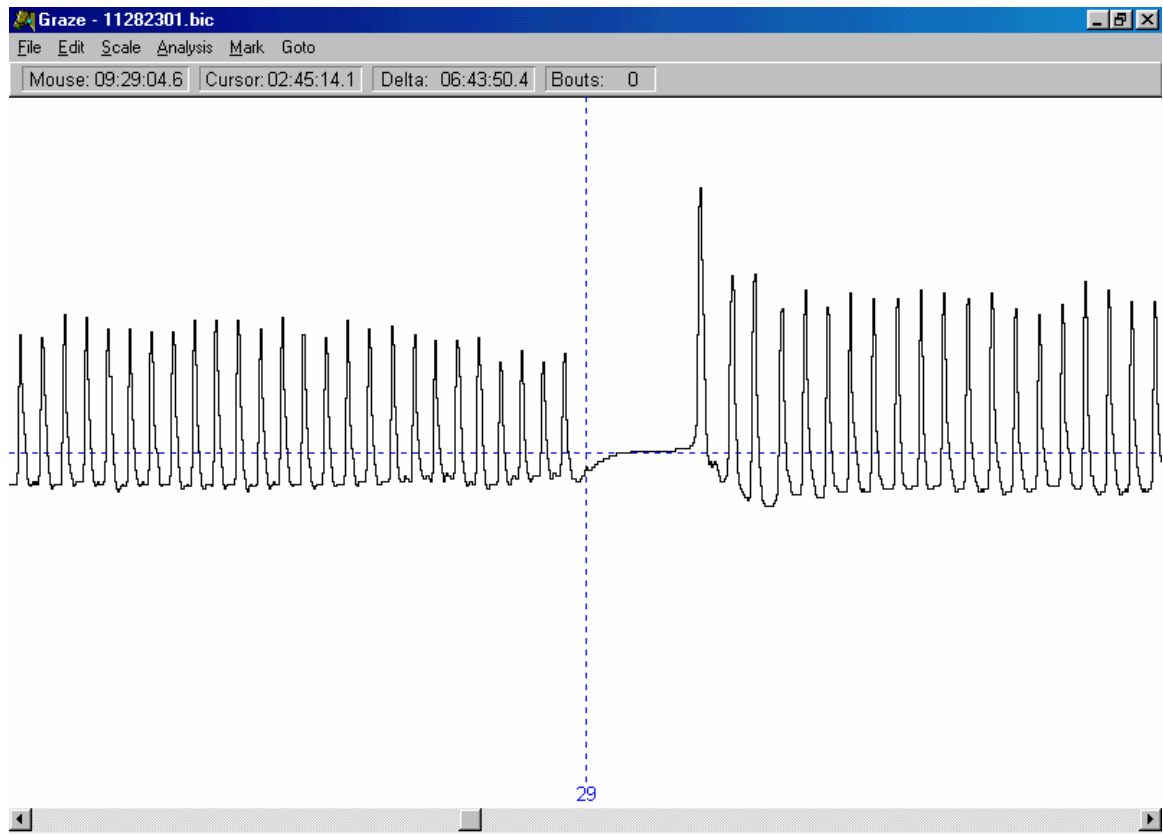


Figure 2-3. An example of the Graze window and recorded ruminating movements in which the wave like patterns separated by brief inactivity marking the movement of boli.



Feed Factors Affecting Chewing Activity

Chemical Structure

The feed offered to lactating dairy cattle is usually heterogeneous in nature, consisting of many different feedstuffs of diverse chemical and physical properties. Plant cell strength is associated with cell wall fibers cellulose, hemicellulose, as well as lignin (Perez-Barbera and Gordon, 1998). Many studies have been carried out in an attempt to investigate the relationship between these components on chewing activity in dairy cattle. Chewing activity is positively correlated to the slowly digestible material in the ration and as a result it has been proposed that NDF is a primary factor in stimulating chewing activity (Welch and Smith, 1969) however, chewing activity per unit of NDF is presumed to vary depending upon forage type (Beauchemin, 1991).

Both total eating and ruminating time on alfalfa silage based diets have been observed to increase by increasing NDF content from 26 to 34 % NDF however, rumination time per kilogram of NDFI was not affected (Beauchemin and Buchanan-Smith, 1989). On barley based diets increasing forage NDF (32, 36 and 40%) resulted in increased total eating and ruminating activities. Conversely, eating but not ruminating time increased when expressed as minutes per kilogram of NDFI (Beauchemin et al., 1994). On corn silage based diets Oba and Allen, (2000) observed that increasing ration NDF level resulted in higher total eating and ruminating time. In that study increasing NDF also increased eating and ruminating efficiency when expressed as minutes per kilogram of DMI, but effects were not observed when expressed as minutes per kilogram of NDFI. Collectively these results suggest that NDF content is a primary factor in stimulating total chewing activity, however source of NDF may result in interactive effects.

Physical Structure

Mastication is the act of physically crushing and shearing feed particles. Feed particle size must be reduced to facilitate swallowing but is also increases rumen degradation. Using *in situ* measurements Beauchemin, (1992) evaluated the effects of chewing during eating on rumen digestion. Unmasticated forage samples and masticated forage samples collected from an

esophageal fistula were incubated in the rumen to determine the potentially digestible fraction, soluble fraction, slowly digestible fraction, rate of disappearance, and lag time for each sample type. Results of the experiment indicated that chewing during eating increased the soluble and potentially digestible fraction but rate of digestion was not different (Table 2-3). It was suggested that the physical rupture of plant tissues during eating and hydration of material from salivation permits rumen microbes to penetrate the epidermis of plant material (Beauchemin, 1992).

As mastication is necessary for consumption of feed, it follows that physical manipulation of feed may affect chewing activities. A number of studies have been carried out in attempt to determine the effect of reducing particle size through grinding (Rodrigue and Allen, 1960), fine chopping (Bailey et al., 1990; Bal et al., 2000; Colenbrander et al., 1991; Gherardi et al., 1992; Grant et al., 1990a; Jaster and Murphy, 1983; Soita et al., 2000; Yang et al., 2001) or pelleting and cubing forage (Beauchemin et al., 1997; Woodford and Murphy, 1988) on chewing activities and feeding behavior. On alfalfa silage based diets both eating and ruminating time was observed to increase with diets of longer mean particle length while rumination time per kilogram of DMI and NDFI was also increased (Grant et al., 1990a). On barley silage based diets increasing particle length resulted in increased total time eating and ruminating, as did eating and ruminating efficiency when expressed as minutes per kilogram of NDFI (Soita et al., 2000). In diets combining alfalfa and barley silage total eating and time spent per kilogram on NDFI increased with increasing particle length but differences in rumination were not observed (Yang et al., 2001b). Differences between eating, ruminating, and total chewing activity (TCA) are often not observed when feeding corn silage of different particle size. Both Bal et al., (2000) and Schwab et al., (2002) observed that fine cut length reduced eating activity but did not effect rumination or total chewing time per kilogram of DMI. Collectively these results suggest that in addition to NDF content, forage particle length is a primary factor in stimulating total chewing activity, even though like NDF, forage source of may result in interactive effects.

Table 2-3. Effects of mastication by heifers on dry matter disappearance of forage during *in situ* measurements (Beauchemin, 1992).

	Unmasticated Forage	Masticated Forage
Potentially Digestible fraction (%)	31.1 ^a	71.6 ^b
Soluble Fraction (%)	16.9 ^a	34.3 ^a
Slowly Digestible Fraction (%)	46.2 ^a	35.8 ^b
Disappearance (%h ⁻¹)	8.25	10.5
Lag Time (h)	1.3 ^a	2.4 ^b

^{a,b} difference between means within each row is significantly different ($P \leq 0.05$)

Nonforage Fiber Sources (NFFS)

Nonforage fiber sources (NFFS) are commonly used as an alternative to forage however they possess inherently different physical and chemical properties. When compared to forage, most NFFS have a larger pool of potentially degradable NDF, smaller particle size, higher specific gravity, and greater passage rate (Firkins, 1997). Nonforage fiber sources possess a high specific gravity, small particles size, and low bulk density (Giger-Reverdin, 2000). Combined, these factors act to decrease likelihood of particle entrapment in the rumen mat, decreasing rumen retention time, digestibility and lastly total chewing activity. Although particle size of NFFS may have greatest effects on reduced chewing activity, the competition between digestion and passage may have interacting effects as well. For example, increasing soybean hulls in the concentrate by 45% resulted in an 8% increase in fractional passage rate while also reducing ruminal NDF digestion (Nakamura and Owen, 1989). Although chewing activity was not measured in this study it follows that if passage rate was increased, the ability of the NDF component to stimulate chewing activity was less than if passage rate had remained constant.

Generally, chewing activity is lower when animals consume diets containing NFFS but rumination time per unit of NDFI has been observed to increase when diets contained excessively low amounts of forage (Beauchemin et al., 1991). When used to substitute forage fiber, the reduction in chewing activity is believed to be largely due the smaller particle size (Mertens, 1992) and has been observed in diets containing cottonseed (Mooney and Allen, 1997), soybean hulls (Weider and Grant, 1994), wet corn gluten feed (Allen and Grant, 2000), oat hulls (Swain and Armentano, 1994), beet pulp, and brewers grain (Clark and Armentano, 1993; Clark and Armentano, 1997). Table 2-4 outlines the effect of NFFS inclusion on eating and ruminating activity. In all reviewed studies, inclusion of NFFS reduced total chewing activity as well as chewing activity expressed as minutes per kilogram of NDFI.

Table 2-4. The effect of NFFS inclusion on diet NDF content, change in total eating and ruminating activity, and eating and ruminating efficiency.

Reference	NFFS ¹	NFFS Inclusion Rate, (%DM)	NDF ³	min/d		min/kg NDFI	
				Eating	Ruminating	Eating	Ruminating
Allen and Grant, 2000	WCGF	24.4	-0.3	-62	-148	-12.4	-26.5
Clark and Armentano, 1993	DDG	12.7	-1.4	-40	-66	-7.0	-11.3
Clark and Armentano, 1997	Beet Pulp	15.7	-1.4	-37	-29	-6.8	-5.4
Clark and Armentano, 1997	Combination ²	32.4	0.9	-76	-60	-19.0	-19.5
Depies and Armentano, 1995	WM	17.0	0.8	-34	-36	-5.8	-7.0
Moony and Allen, 1997	Cottonseed	11.9	1.4	-32	-10	-7.9	-7.2
Weider and Grant, 1994	Soybean Hulls	18.0	3.8	-45	-122	-10.6	-25.2

¹WCGF = wet corn gluten feed, DDG = distillers dried grain, WM = wheat middlings

² 8.6%DM whole cottonseed, 10.2%DM distillers dried grains, 13.6% DM wheat middlings

³ difference between control diet NDF content and treatment (containing NFFS) diet NDF content

Passage Rate and Particle Size Dynamics

Particle size has resulting effects on passage of material through the digestive tract of ruminants (Wilson and Kennedy 1996; Okine et al., 1990). Particle size is a direct result of processing the feed before it is offered to the animal however further breakdown of the material occurs during mastication and rumination (Fisher and Burns 1987; Kusmartono et al., 1996) while little particle size reduction occurs during either rumen fermentation or digestion (Okine and Mathison 1991; McLeod and Minson 1988; Murphy and Nicoletti 1983).

Resistance to flow of particles from the reticulorumen increases with increasing particle size (Poppi et al., 1985; Dixon and Milligan 1985) resulting in slower passage rates. Figure 2-4. illustrates the effect of particle size on resistance to flow from the rumen using both grass and legume samples. Poppi et al., (1980) collected digesta passing out of the reticulorumen and material was subsequently sieved through a series of mesh screens. Although there was no sharp division between particles that could and could not leave the rumen, an inflection point appeared at 1.18 mm.

Various authors have attempted to partition the particle size distribution into groups based on passage dynamics (Spalinger and Robins 1992; Illius and Gordon 1991; McLeod and Minson 1988; Poppi et al., 1981;). Large particles (LP) can be defined as those that have a low probability of ruminal escape while small particles (SP) being without physical limitation merely require ruminal contractions to be impelled through the reticulorumen. (Wilson and Kennedy 1996; McLeod and Minson 1988 a,b). As mentioned Poppi et al., (1980) proposed the critical size theory which surmised that particles retained on a 1.18 mm aperture sieve meet a high resistance to passage out of the rumen and may be labeled as LP as a rise in resistance of particles leaving the rumen was associated with increasing particle size. (Poppi, 1981 a,b,c; Poppi et al., 1980). Critics argue that the critical size theory is an over simplification, which erroneously implies all SP (i.e. < 1.18 mm) flow out of the rumen with equal resistance. Cardoza (1985) and Shaver (1988) disagreed with the findings of Poppi (1980) citing the critical size of 1.18 mm was found using sheep and reported that the critical size may be different for cattle possibly closer to 3.6 mm with difference due to the size of the animal itself (Van Soest 1996). Wilson and Kennedy (1996)

indicted that fiber particulate matter clears the rumen at a rate proportional to the inverse function of the particle size (see Figure 2-5). Both forage form and type have profound effects on the rate of passage rates of sheep digesta. When fed ground or chopped alfalfa hay, or chopped straw is fed the rate of clearance for the smallest particles (retained on a 1.50 mm sieve) varied by a factor of 3, in contrast the passage rate of large particles were similar for all treatments. These results indicate that the passage rate of digesta is complex with forage type, particle size distribution, and the botanical nature of forage playing governing roles.

Recently Yang et al., 2001 fed diets of different particle size and noted that a large proportion of rumen digesta particles passes through a 1.18 mm screen and that particle size reduction was not the sole rate limiting step in clearance out of the reticulorumen however the larger proportion of particles ≤ 1.18 mm indicated that reduction in particle size was an important factor in influencing passage of digesta out of the rumen. As a result that it is likely the a multitude of factors such as level of intake (Allen 1996; Cardoza and Mertens 1986) plant tissue origin, buoyancy, and specific gravity, particle density may have influencing effects on passage of particles out of the rumen (Trinacty et al., 1999; Wilson and Kennedy, 1996). It is likely that even if resistance to particles passing out of the rumen is lowest when less than 1.18 mm in length entrapment of these particles into the rumen mat can occur. Observation of particles > 3.35 mm in duodenal digesta and feces by these authors suggests that longer particles, although less likely, do indeed pass out of the rumen.

Figure 2-4. The mean relative resistance to flow of grass and legume hay particles from the rumen of sheep (Poppi et al., 1980)

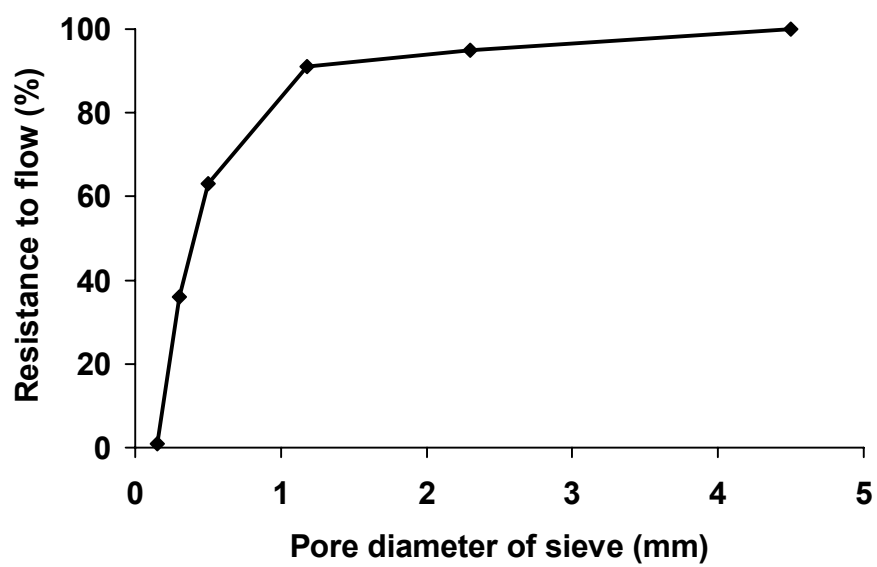
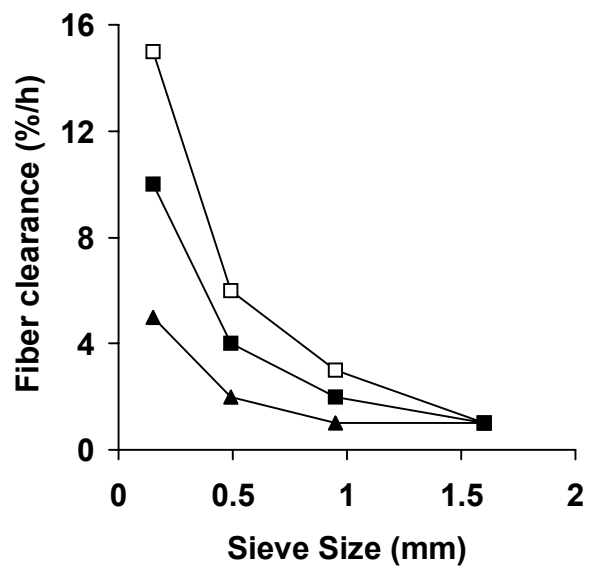


Figure 2-5. Relationship between digesta particle size and fiber clearance rate from the reticulorumen of sheep fed three different forages (□) ground alfalfa, (■) chopped alfalfa, (▲) chopped straw (Wilson and Kennedy, 1996).



Effects of Feeding Ruminants Forage of Different Particle Size

Rumen Fermentation, pH, and Digestion

Complete understanding of the dynamic nature of ruminal fermentation is difficult due to the multitude of factors in action. Although a number of studies have been designed in an attempt to further understand the effects of particle size on ruminal fermentation little uniformity exists (see 2-5 and 2-6). In a review of published studies examining the effects of different theoretical cut lengths (TLC) of alfalfa silage and corn silage, no significant differences were observed in dry matter digestibility. Of the studies reviewed, dry matter digestibility did not appear to be linked to different cut lengths of silages however differences have been observed when forages are finely ground or when dehydrated forms are fed (Beauchemin et al., 1997; Rodrigue and Allen, 1960).

Increasing particle size may result in increased rumination activity and higher mean rumen pH values. Grant et al., (1990a) harvested alfalfa silage based rations of three different lengths (geometric mean = 2.6, 2.8, and 3.0 mm) and observed a 0.8% increase milk fat percentage (3.0 versus 3.8%), and pH increased of 0.7 units (5.3 versus 6.0) when long forage was compared to short treatments. Although there is some evidence showing that forage cut length effects rumen pH and volatile fatty acid level, additional work should be carried out to determine how particle size may be important when feeding cows in different stages of lactation or in diets including varying levels on non-forage fiber sources. Additionally, diets of coarse particle size may result in an increased tendency of sorting, it is likely that even if mean rumen pH and VFA values are not different, diurnal patterns may in variation on ruminal fermentation patterns.

Dry Matter Intake

The effect of particle size on feed intake is unclear with conflicting results being reported (Kennedy and Doyle 1993). Difficulty in interpreting the response of particle size on DMI may be in part due to digestibility and specific gravity, factors independent of the individual feeds particle size (Dulphy and Van Os 1996). When detected, intake response to reduce particle size is usually positive with the magnitude depending upon the extent of particle reduction as well as the type and digestibility of forage fed. Welch (1967) inserted 7-cm polypropylene ribbons into the

reticulorumen of sheep feed chopped alfalfa hay and reduced DMI by 30 %. Increasing the length of the ribbons to 30-cm reduced intake by 75 %. When inserting the same weight in ground ribbons no effect on intake was noted. Positive effects with reduced particle size have been noted in many poor quality forages containing high cell wall contents (Kusmartono et al., 1996; Panditharane 1988; Troelsen and Bigsby 1968; Minson 1967; Heaney et al., 1963). Difficulty in interpreting the response of particle size on DMI may also be a result of interactive factors such as digestibility, specific gravity, and animal nutrient requirements (Dulphy and Van Os, 1996).

Few authors have observed effects of alfalfa silage on intake when well-balanced rations are fed to mid-lactation cows (see Table 2-5). Positive effects with reduced particle size on DMI have been reported in some studies feeding corn silage of different particle size (Stockdale and Beavis, 1994) but have not been observed in others (see Table 2-6). Furthermore the degree of particle size reduction varies depending upon processing and particle size determination methods used, making treatment types difficult to quantify in relation to others. Although several authors have reported increased DMI with reduced particle size while feeding high quality forages (Beauchemin 1997) most authors report that no effect on DMI occurs when good quality forage is fed alone or included in a ration meeting NRC requirements (see Tables 2-5 and 2-6). Literature appears to support the hypothesis that DMI is influenced by particle size reduction only when a poorly digestibility feed with a high cell wall content is fed and no effects occur when good quality forages are fed.

Milk Production and Composition

In alfalfa based diets, forage particle size has been shown to significantly affect both yield and composition however most differences are reported when forage is in the dehydrated form (Woodford and Murphy 1988; Shaver 1986; Beauchemin et al., 1997). When forage was silage form and different lengths of cut were fed differences have been observed in milk fat (Grant et al., 1990a; Fisher et al., 1994; Shaver et al., 1996) and protein percentages (Beauchemin et al., 1994) but have not been observed in others (Armentano et al., 1988; Colenbrander et al., 1991).

Of the studies reviewed none reported a significant response in milk production or FCM from feeding corn silage of different particle size (Clark and Armentano, 1999, Bal et al., 2000). Increasing milk protein with decreased corn silage particle size has been observed in some studies and believed to be a result of increased starch and in essence, energy availability (Clark and Armentano, 1999). Fat percentage does not appear to be affected by feeding rations of different corn silage particle size (Clark and Armentano, 1999; Stockdale and Beavis, 1994) however in one study in which coarse particle size (TLC = 1.90 cm) resulted in excessive amounts of sorting and NDF refusal milk fat was actually higher in rations of shorter particle size (Bal et al., 2000).

Although significant effects of particle size on TCA accompany effects on rumen pH (Grant et al., 1990a; Shaver et al., 1988; Woodford and Murphy, 1986), differences are small and are not likely to result in large shifts in volatile fatty acid production required to alter milk fat composition. Observed differences in composition are more likely to be a result of other factors such as passage and rate or extent of digestion.

Biology of Milk Fat Depression

Similar to most agricultural products, the value of milk is determined by its aggregate components, namely fat, protein, lactose, minerals, and trace elements (Manfredini and Massari, 1990). Fat is a highly variable component of bovine milk and may vary over three percentage units depending upon the ration consumed (Bachman, 1992). As a means to meet the high-energy demands of the lactating dairy cow, rations high in concentrate and NSC are commonly fed (Allen, 1997). As the amount of grain increases milk fat levels typically decline (Gaynor et al., 1995; Xu et al., 1994).

The primary components of milk fat are triglycerides (97.0 – 98.0%). Other lipids contained in milk include diacylglycerides (0.25 – 0.48%), monoacylglycerides (0.02 – 0.04%), phospholipids (0.6 – 1.0%), cholesterol (0.2 – 0.4%), glycolipids (0.006%) and free fatty acids (0.1 – 0.4% (Collier, 1985). Approximately one half of the fat sources for milk originate from the uptake of preformed fatty acids arising from three sources; lipids of dietary origin, those mobilized from

Table 2-5. The effect of reducing alfalfa particle size on digestive parameters and milk production in lactating cattle

Reference	DMI ⁶	Ruminating (min/d) ⁶	DMD	Acetate: Propionate ⁶	PH ^{6,7}	Yield	FCM ⁶	% Protein ⁶	% Fat ⁶
Beauchemin et al., 1994 ¹	+	-	N/A	N/A	N/A	NS	NS	+	--
Yang et al., 2001 ²	NS	N/A	NS	NS	NS	NS	--	+	-
Fischer et al., 1994 ³	+	NS	N/A	NS	NS	NS	-	NS	-
Grant et al., 1990 a ⁴	NS	-	N/A	-	--	NS	-	NS	--
Woodford et al., 1986 ⁵	NS	NS	NS	NS	NS	NS	NS	NS	NS

¹ treatments were composed of feeding long alfalfa hay at different levels (0, 10, 20 % DM) and different theoretical length of cut (TLC): 0.5 cm and 1.0 cm.

² treatments were composed of feeding barley silage, alfalfa silage, and alfalfa hay of different particle size: control (cut length not specified) and rechopped using a 4.0-mm recutter screen.

³ treatments were composed of feeding long alfalfa hay at different levels (0, 3 kg/d) and alfalfa silage of different TLC: 0.46 cm and 0.95 cm.

⁴ treatments were composed of feeding alfalfa silage of different TLC: 0.48 cm with a 7.5 cm recutter screen and 0.95 cm no recutter screen.

⁵ treatments were composed of diets of different mean particle length (0.26, 0.46, 0.64, and 0.90 mm) as measured by an oscillating screen particle separator.

⁶ + denotes significant reducing effect (if + then $P \leq 0.05$); - denotes significant increasing effect (if - then $P \leq 0.05$, if -- then $P \leq 0.10$), NS = not significant $P < 0.10$.

⁷ mean pH.

Table 2-6. The effect of corn silage particle size on digestive parameters and milk production in lactating cattle

Reference	DMI ⁶	Ruminating (min/d)	DMD	Acetate: Propionate	pH ⁷	Yield	FCM	% Protein	%Fat
Bal et al., 2000 ¹	NS	NS	NS	NS	NS	NS	NS	NS	NS
Schwab et al., 2002 ²	NS	NS	N/A	N/A	N/A	NS	NS	NS	NS
Stockdale and Beavis, 1994 ³	+	N/A	NS	NS	NS	NS	NS	NS	NS
Clark and Armentano 1999 ⁴	NS	NS	N/A	N/A	N/A	NS	NS	NS	NS
Odai et al., 1988 a,b ⁵	NS	N/A	NS	NS	N/A	NS	NS	NS	NS

¹ treatments were composed of feeding corn silage of different theoretical length of cut (TLC): 0.95 cm, 1.45 cm, and 1.90 cm.

² treatments were composed of feeding corn silage of different TLC: 1.30 cm, 1.90 cm, and 3.20 cm.

³ treatments were composed of feeding corn silage harvested with screen apertures of 9.0 cm², 36.0 cm², or no screen.

⁴ treatments were composed of feeding harvested corn silage (TLC not specified) or rechopped using a 3.3 cm screen.

⁵ treatments were composed of feeding corn silage of different TLC: 0.60 cm, 2.40 cm.

⁶ + denotes significant reducing effect ($P \leq 0.05$).

⁷ mean pH.

adipose tissue and lastly those synthesized in the liver. The remaining half is a result of de novo synthesis from acetate and β -hydroxybutrate, which arise from rumen microbial fermentation.

A multitude of nutritional and non-nutritional factors affecting milk fat concentrations have been identified but nutrition is believed to be the predominate environmental factor. Although not a pathological condition, milk fat depression (MFD) is of interest due to its impact on milk quality and value. Scientific evaluation of MFD has occurred for over several decades and resulted in a number of theories but a single universal theory has yet to be accepted (Bauman and Griinari, 2001). Although the complexity of MFD may be a result of a multitude a factors, diets containing high levels of grain and low roughage are commonly observed in milk fat depression (Armentano and Pereira, 1997; Rodrigue and Allen, 1960). It is commonly believed that diets of this type are lacking in the amount of fiber necessary to be effective in maintaining normal rumen function (Mertens, 1997). Two nutritional explanations for this have received considerable attention; one, a shortage in the supply of lipid precursors to the mammary gland and two, a direct inhibition on pathways occurring in the mammary tissue. The glucogenic theory has historically been used to explain MFD while very recently the trans fatty acid hypothesis has been strengthened.

The Glucogenic-Insulin Theory

Reduced milk fat from finely chopped silage has historically believed to be a result of reduced chewing activity, salivary buffer secretion, altering both ruminal fermentation and glucose metabolism. The linking of these factors to MFD is associated with glucogenic-insulin theory (Grant et al., 1990a). Table 2-7 contains data from a classical experiment often cited when describing the effects of feeding silage of reduced particle size (Grant et al., 1990a). In the study eighteen cows were fed one of three TMR containing forage differing in physical structure and outlined the effects on chewing activity, rumen fermentation, blood plasma and milk production. Cows were fed a TMR containing forage of fine (theoretical cut length = 0.48 cm), coarse (theoretical cut length = 0.95 cm) or medium (1:1 mixture of the fine and coarse) physical structure. Reducing forage particle size resulted in no effects on DMI but reduced chewing activity, acetate to propionate ratio and milk fat percentage. According to the theory first proposed

by McClymont and Vallance, (1962), higher propionate and glucose levels stimulate insulin release by the pancreas. Insulin is then proposed to stimulate lipase activity to enhance uptake of lipogenic precursors, and to decrease the release of fatty acids from the adipose tissue. As a result the mammary gland becomes limited in acetate and preformed fatty acids which are required for milk fat synthesis (Griinari et al., 1997b; McGuire et al., 1995). Therefore according to the glucogenic theory of MFD, both mammary tissue and adipose tissue compete for nutrients but in times of elevated circulating insulin, nutrients are shunted towards adipose tissue (McGuire et al., 1995).

In order to isolate and study the effects of insulin on milk yield and composition McGuire et al., (1995) employed the hyperinsulinemic-euglycemic clamp technique in a study using lactating dairy cows. Insulin was continuously infused via the jugular vein at a rate of 1ug/kg BW per hour. Plasma insulin concentrations were elevated from 1.5 ng/mL during baseline period to 7.8 ng/mL. In the study glycemia was maintained within a range of 10% of normal blood glucose levels with glucose infusion rates of 84.8 g/h maintaining the euglycemic state. The hyperinsulinemic-euglycemic clamp is useful in evaluating the validity of the glucogenic-insulin theory as it elevates blood insulin 2 - 5 fold, levels commonly observed in animals experiencing MFD. The induced hyperinsulinemia and infusion of glucose elevates adipose tissue uptake of lipogenic precursors (acetate and β -hydroxybutyrate) and activates lipoprotein lipase to increase uptake of preformed fatty acids. Lastly the technique minimizes fatty acids derived from adipose tissue as rate of lipolysis is minimized (McGuire et al., 1995; Mackle et al., 1998). Results of the study are listed in Table 2-8. Although DMI declined on the fourth day after insertion of the clamp, milk yield did not change, indicating that the mammary gland is not sensitive to insulin. More importantly, there were no significant differences in milk fat concentration from cattle on elevated treatments. Similar results obtained in an additional study (Griinari et al., 1997) strengthen the conclusion of McGuire et al., (1995) that the glucogenic-insulin theory is incapable of explaining MFD.

Table 2-7. The effect of alfalfa silage cut length on chewing activity, rumen fermentation, plasma glucose and serum levels, and milk production on dairy cows fed a 50:50 forage to concentrate TMR (Grant et al., 1990a).

	Forage Structure ¹			P-Value
	Fine	Medium	Coarse	
Dry Matter Intake, kg	22.4	22.0	22.2	0.88
Total Chewing Activity, min/d	570	671	735	< 0.05
Rumen pH	5.3	5.9	6.0	0.10
Rumen VFA, mol/100 mol				
Acetate	58.3	61.2	61.8	< 0.05
Propionate	22.3	20.2	19.5	< 0.05
A:P	2.77	3.13	3.52	< 0.05
Blood				
Glucose (mg/dL)	65.9	54.0	44.9	< 0.05
Insulin (ng/mL)	0.30	0.26	0.20	< 0.05
Milk				
Yield, kg/d	31.5	32.1	31.1	0.56
4% FCM, kg/d	27.5	30.3	29.5	< 0.05
Fat, %	3.0	3.6	3.8	< 0.05
Protein, %	3.0	3.0	3.1	0.14

¹ Dietary treatments contained alfalfa haylage of different particle size that was harvested at different theoretical length of cut settings (Fine = 0.48 cm with a 7.5 cm recutter screen Coarse = 0.95 cm no recutter screen) or in the case of MEDIUM a 1:1 mixture of Fine and Coarse forages.

Table 2-8. Milk yield and composition from cows at baseline insulin levels equipped with a hyperinsulinemic-euglycemic clamp (McGuire et al., (1995).

	Baseline	Insulin Clamp
Milk kg/d	32.4	33.6
Fat, %	3.85	3.66
Protein, %	1.26	1.22
Yield in milk, kg/d		
Fat	3.04	3.14
Protein	0.98	1.05

Trans Fatty Acid Hypothesis of Milk Fat Depression

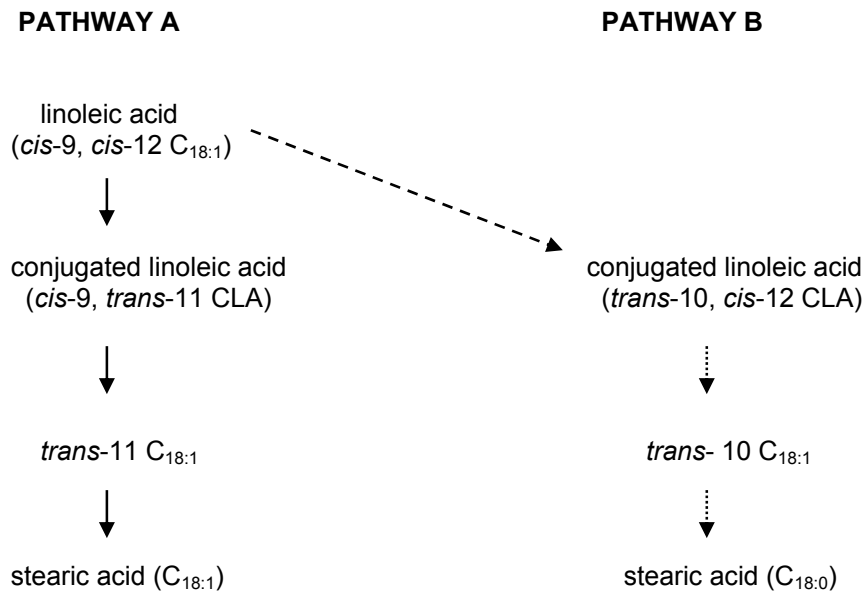
In contrast to the glucogenic-insulin theory, the trans fatty acid hypothesis speculates that specific polyunsaturated fatty acids resulting from incomplete biohydrogenation during rumen fermentation impedes mammary fat synthesis (Davis and Brown, 1970). Until very recently only *Butyrivibrio fibrisolvens* was known to be capable of biohydrogenation. However, more recently it has been noted that a range of bacteria are responsible for biohydrogenation and that no single species catalyzes the complete biohydrogenation sequence (Harfoot and Hazlewood, 1997).

Of a variety of compounds receiving attention, trans-octadecenoic acids (trans C_{18:1}) recently have been studied due to observed increases when milk fat is depressed (Emory, 1973; Gaynor et al., 1995). Elevated milk levels of trans-C_{18:1} fatty acids in cows experiencing MFD was first observed by Storry and Rook (1965), however Davis and Brown (1970) were the first to suggest a possible relation between trans-C_{18:1} and MFD.

Lipids of forage origin primarily consist of glycolipids and phospholipids with unsaturated fatty acids being linolenic (C_{18:3}) and linoleic (C_{18:2}) acid. In comparison lipid composition of that associated with grains is predominately triglycerides containing linoleic and oleic (cis-9 C_{18:1}). Once feed is consumed, rumen microbes first hydrolyze ester linkages by microbial lipolytic enzymes. Subsequent hydrolysis, biohydrogenation of unsaturated fatty acids appears to be carried out almost exclusively by bacteria (Singh and Hawke, 1979). Common to biohydrogenation of both α -linolenic and linoleic (Figure 2-6) is pathway A illustrated in Figure 2-6 in which an initial isomerization step follows the formation of *cis*-9, *trans*-11 C_{18:1} and finally results in *trans*-11 C_{18:1}.

There is increasing evidence that factors affecting rumen biohydrogenation affect milk fat production and may in part explain MFD. Gaynor et al., (1995) demonstrated that cows fed high grain diets produced milk high in *trans* C_{18:1} fatty acids, a result of incomplete biohydrogenation in the rumen. Through the addition of a dietary buffer to a high concentrate diet, Kalscheur et al., (1997) was able to alter rumen fermentation, depress *trans* C_{18:1} production in milk (5.8 vs. 3.0%) and ultimately increase milk fat levels (4.22 vs. 3.91%). Lastly, Griinari et al., (1998) reported that

Figure 2-6. Proposed pathway of ruminal biohydrogenation of linoleic acid (Bauman and Griinari, 2001).



feeding a diet high in concentrate and low in fiber results in an change in the *trans* C_{18:1} concentration in milk. Similar to feeding studies, Gaynor et al., (1994) demonstrated that percent milk fat declined when *trans* C_{18:1} fatty acid isomers were infused into the abomasum (Table 2-9). This is concurrent with various other observations that infusion of C_{18:1} dramatically decreased milk fat yield (Chouinard et al., 1999; Looor and Herbein, 1998).

Until very recently most studies evaluating the *trans* fatty acid hypothesis were composed of treatments containing a mixture of isomers however there is growing speculation that the concentration of *trans*-10 C_{18:1} alone may have large effects on milk fat synthesis (Griinari et al., (1997). Here it is believed that rumen fermentation is altered so that a portion of the unsaturated fatty acids are biohydrogenated via pathway B (Figure 2-6) resulting in increases of *trans* -10 C_{18:1}. Testing the effects of various isomers, Baumgard et al., (2000) hypothesized that isomers containing the *trans*-10 double bond may be the cause of MFD. Figure 2-7 illustrates the study in which effects of abomasal infusions of *cis*-9, *trans*-11, and *trans*-10, *cis*-12 on milk fat percentage were evaluated. Results of the experiment indicated that 4 day infusion of *cis*-9, *trans*-11 CLA isomer had no effects but infusion of less than 10g/d of *trans*-10, *cis*-12 reduced milk fat percentage by 40% (Baumgard et al., 2000). As a result of these and other studies there is growing speculation that shifts in rumen biohydrogenation resulting in *trans*-10 C_{18:1} and *trans*-10, *cis*-12 C_{18:1} rather than *cis*-9, *trans*-11 C_{18:1} may result in MFD (Griinari et al., 1998, 1999).

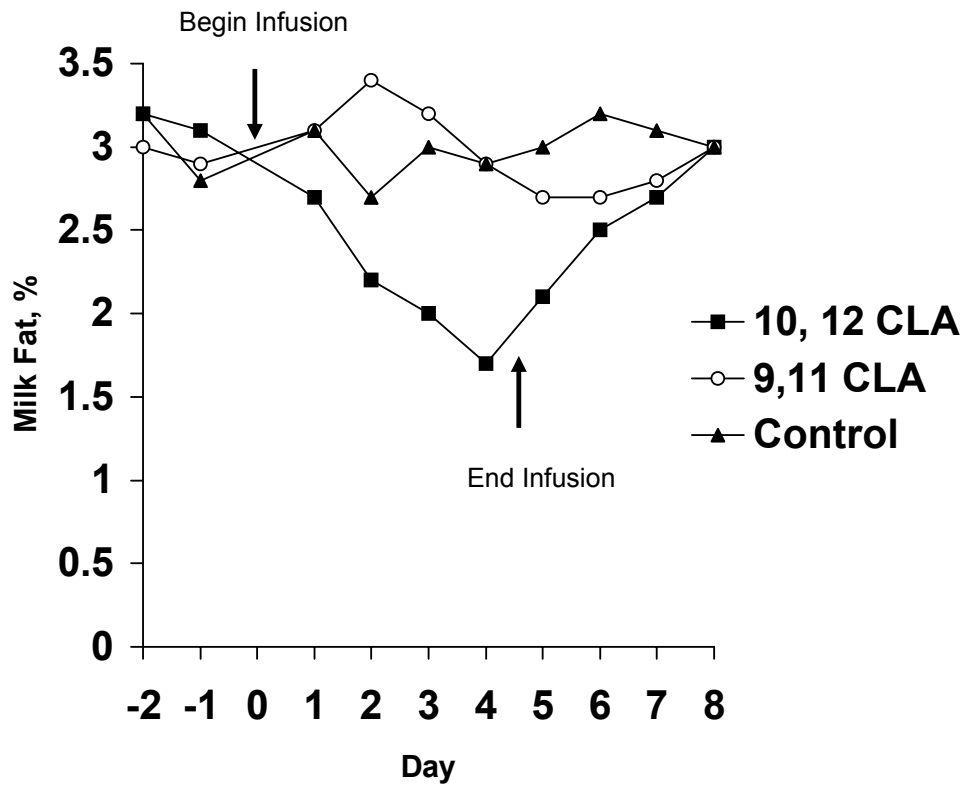
TMR Particle Size and Milk Fat

It is commonly believed that diet is a major factor influencing the C_{18:1} concentration in bovine milk fat and ultimately effects on MFD. More specifically, dietary changes such as increases in grain content, decreases in rumen pH and increase concentration of *trans* C_{18:1} fatty acids in the rumen and milk (Chouinard et al., 1998). Unfortunately a complete understanding of factors affecting rumen biohydrogenation, *trans* C_{18:1} fatty acids production, and specific mechanisms associated with milk fat depression are not fully understood. As mentioned it has been clearly demonstrated that feed particle size results in a decrease in milk fat production and

Table 2-9. The effect of post ruminal C_{18:1} infusion on milk yield and composition. (Gaynor et al., 1993).

	control	trans
Milk, kg/d	47.0	47.0
Fat, %	3.45	2.59
Protein, %	3.08	3.06
Lactose, %	4.93	4.85
Total Solids, %	12.16	11.15
Fatty Acid, g/100g		
<i>cis</i> -C _{18:1}	23.3	31.7
<i>trans</i> -C _{18:1}	1.9	8.0

Figure 2-7. The effect of abomasal infusion of *cis*-9, *trans*-11 or *trans*-11, *cis*-12 conjugated linoleic acid (CLA) isomers on temporal pattern of milk fat (■) 10, 12 CLA, (○) 9,11 CLA (▲) control (Baumgard et al., (2000).



in some cases MFD. The effect of ration particle size on rumen biohydrogenation is not fully understood. It has been demonstrated that rations that result in low rumen pH, while maintaining a consistent level and dietary lipid results in an increase of the *trans*-10 C_{18:1} in milk. As a consequence of these results it could be suggested that diets that result in low rumen pH, such as those containing finely chopped forages shift rumen biohydrogenation to Pathway B (Figure 2-6) and result in increase of the *trans*-10 C_{18:1} which ultimately results in effects as observed by Baumgard et al., (2000). Although the effect of rumen pH is largely speculated upon as a factor in MFD, other dietary factors such as intake, digesta passage rate, and substrate concentration may also have primary or interactive effects on the extent and rate of biohydrogenation in the rumen and possibly result in MFD. Lastly, Harfoot and Hazlewood et al., (1997) note that, “there is clearly much research to be done regarding the physical relationship between bacteria, food particles, and lipid in the rumen and the effect of this on lipid metabolism.”

In summary, recent studies using a hyperinsulinemic-euglycemic clamp (McGuire et al., 1995; Gaynor et al., 1995; Griinari et al., 1997a and b) appear to suggest that MFD cannot be explained by the glycogenic insulin theory. These studies found no effect of circulating insulin levels on either milk yield or fat levels. It is therefore most likely that mammary and adipose tissues do compete for nutrients, circulating insulin levels are not responsible for shifting the nutrient balance towards adipose tissue (McGuire et al., 1995). Currently the trans fatty acid hypothesis, which attributed MFD to the putative inhibition of fat synthesis, shows greater promise in elucidating the cause of MFD.

Particle Size and Effective Fiber

Fiber is defined as the slowly digestible or indigestible organic fraction of the diet that occupies space in the gastrointestinal tract (Mertens 1997). Cole and Mead (1948) were the first to note that coarse fiber is required by ruminants and without it a, “physical deficiency ... results in the following syndrome: failure of, or diminished rumination; difficulty in eructation, often causing tympany or bloat, ... reduction in food consumption in cattle; and depraved appetite.” The coarse fiber portion of the ration is believed to be *effective* in stimulating chewing activity and

salivary buffer production as well as increasing rumen pH and acetate to propionate ratio; all factors critical in animal overall performance and milk production (Allen 1997). Although the extent of physical effectiveness is likely related to a host of factors such as DMI (Wilson and Kennedy 1996), NSC content (Beauchemin, et al., 1997 b; Nocek and Russell 1988), particle size distribution (Poppi et al., 1980), particle shape (Luginbuhl, 1991), particle fragility (Kennedy, 1997; Iwaasa, 1996), moisture (Porter and Barton 1997), specific gravity (Stetter Neel 1995; Wattiaux et al., 1993), cation exchange capacity (Tingxian, 1996; McBurney et al., 1986; McBurney et al., 1986), buffering ability (Tucker et al., 1992), and rate of fermentation (Weimer 1996; Mertens 1997), the fiber and physical component of the diet are believed to have primary effects.

Several researchers have proposed methods designed to measure the effective fiber portion of the diet (Allen, 1997; Armentano and Pereira 1997; Grant, 1997; Firkins, 1997; Mertens, 1997). Effective NDF (eNDF) has been defined as the ability of a feed to replace the roughage in a ration while maintaining milk fat percentage (Armentano and Pereira 1997). Physically effective NDF (peNDF) was defined as that fiber portion of the diet that stimulated chewing activity and responsible for formation of the rumen mat (Mertens, 1996; Mertens, 2000).

Milk fat percentage is commonly used as an indicator for effective fiber as it has proven to be an indicator of optimal rumen fermentation and ruminal pH levels (Armentano and Pereira, 1997). By measuring the rate of change in milk fat percent, Clark and Armentano (1993) estimated eNDF of diets differing in particle size. Recently there has been criticism of using milk fat as a sole indicator of fiber effectiveness as effectiveness values have not been repeatable across different feed types. Additionally, when using milk fat as a response, cows in mid lactation are most often used, as they are more responsive to dietary changes than cows in early lactation and as a result changes in milk fat may be more difficult to detect (Allen, 1997). Beauchemin et al., (1997) found that processing forages reduced rumination time by 52 – 62 % along with rumen pH while only minimal effects on milk fat percentages were observed. Lastly, Mertens, (2000) noted that changes in milk fat may not be observed in groups of animals with poor rumen function and overall animal health, and as a result milk fat depression may not be the best indicator of

effectiveness of fiber in the ration. As a result it can be suggested that fat content alone is not a suitable indicator of effective fiber in the ration.

The primary animal response variable associated with the measurement of peNDF is total chewing activity (sum of eating and ruminating) per unit of NDFI (Mertens, 2000). The peNDF portion of the ration is believed to be highly resistant to passage out of the rumen, and as a result stimulates chewing, saliva secretion and rumen mat formation; all factors that ultimately maintain rumen pH (Mertens, 1997). The critical size theory has been adopted into the peNDF system, as it hypothesized that particles ≥ 1.18 mm have the greatest resistance of passage and largely responsible for stimulating of chewing and rumination (Poppi et al., 1980). As a result, the peNDF portion of the ration is estimated as the amount of NDF retained, on a 1.18 mm screen from dry sieving (Mertens, 1997). In order to investigate the effects of peNDF on rumen pH Pitt et al., (1996) compiled data from sheep, beef and dairy cattle studies and determined that the relationship was curvilinear reaching a plateau near a pH of 6.5 – 6.7. Recently, Yang et al., (2001) observed that reducing forage particle size reduced total chewing activity (720 vs. 684 min/d) however even though mean pH was numerically lower for shorter diets (6.09 vs. 5.99); differences were not statistically significant ($P > 0.05$). Although a lack of direct effect was reported, it is likely that the magnitude of effects observed will depend upon the magnitude of differences in particle size between treatments themselves. More specifically, differences in ration particle size as measured by the PSPS were small (amount of dry matter retained on the 19.0 mm, 8.0 mm and pan for the short treatment was 4.5, 34.6, and 60.9 % DM, compared to 0.3, 32.2, and 67.5 % on the long treatment) and as a result differences in feeding behavior, intake and nutrient utilization would be reflected accordingly.

Developing a framework for routine laboratory measurement of ration peNDF concentration has been proposed by Mertens, (2000) but not yet detailed. It has been suggested that chemically NDF be determined according to the procedure of Van Soest et al., (1991) but modified to include to include heat stable alpha-amylase. Currently methods used to measure particle size for peNDF determination have not been standardized but the PSPS has been suggested along with other commonly used sieving devices. Although few experiments have

been conducted to investigate the effects of feeding rations of different peNDF on chewing activity and rumen pH, Mertens (1997) suggested that a minimum of 21 % peNDF was required to adequately stimulate chewing activity required to maintain an average rumen pH of greater than 6.0 (Table 2-10). Currently more research is needed to 1) evaluate the peNDF system and the potential value to improving current fiber recommendations; 2) evaluate the use of the PSPS for measurement of peNDF; 3) evaluate the effects of forage particle size on peNDF values; 4) evaluate the effects of feeding feeds of different particle size on chewing activities and rumen fermentation.

Table 2-10. Estimating the physically effective neutral detergent fiber (peNDF) required maintaining a specified ruminal pH of lactating cows (Mertens, 1997).

Ruminal pH	peNDF (kg/d)	Ration peNDF (%DM)
5.9	3.66	19.3
6.0	4.40	22.3
6.1	5.25	25.6
6.2	6.32	30.0

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