Röbäcksdalen meddelar

Voluntary feed intake by dairy cattle
With special emphasis on the effects of interactions between fibre and starch quality in the diet

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Introductory paper
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List of abbreviations

DM = Dry Matter
DMI = Dry Matter Intake
NDF = Neutral Detergent Fibre
NDFD = Neutral Detergent Fibre Digestibility
VFA = Volatile Fatty Acid
NSC = Non Structural Carbohydrates
OM = Organic Matter

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1. Abstract

Feed intake is regulated and limited by the physical and metabolic requirements of animals. Physical control of voluntary dry matter intake (DMI) in high productivity dairy cows is, to a large extent, dependent on the reticulo-rumen capacity/volume. Physical fill is thought to be mainly determined by the rate of digestion of feed, the passage rate and the fill effect of the diet. The neutral detergent fibre (NDF) and water contents of feed, reticulo-rumen motility, reticulo-rumen volume, and neutral detergent fibre digestibility (NDFD) in the rumen are the main factors controlling physical regulation. When the energy or protein requirements of dairy cows are met by the feed, then further intake is stopped/depressed as a result of feedback via a message from the satiety centre within the central nervous system.

Volatile fatty acids (VFA) are produced as a result of microbial degradation of feed in the rumen. The amount of each acid produced and absorbed has both an individual and a combined effect (as a part of the mixture of acids) on the regulation of the voluntary intake of feed. Propionate is the most important of all VFA since it enhances the release of insulin into the blood which, stops further intake of energy from feed. Glucose on the other hand, has little or no role in the control of feed intake in ruminants. Diets that are highly fermentable in the rumen produce instant VFA and the titratable acidity of these has very strong inhibitory effects on reticulo-rumen motility, causing rumen stasis and cessation of further intake. Starch from cereal grains is normally added to the diets of high productivity dairy cows to meet the energy requirements for milk yield.

Rapid degradation of starch has a negative impact on the rumen and total tract digestibility of fibre. Starch rumen digestibility and availability depends on the type of cereals and the type and intensity of any processing that they have undergone. Grass and legume silage cut and ensilaged at early maturity is associated with increased intake and digestibility of NDF and organic matter (OM) although it is reported that such silages regulate feed intake metabolically rather than physically. However, the chemical composition and physical characteristics change as the plant matures. A number of models have been proposed for predicting intake; their accuracies vary. Possible strategies for improving energy utilization from starch and increasing voluntary feed intake include: shifting the site of starch digestion from the rumen to the small intestine through the use of processed cereals (*e. g.* physical processing); selecting correct cereal type; and determining the optimum level of maturity of forages (grasses and legumes)
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2. Introduction

High yielding dairy cows must consume large amounts of feed to provide the necessary nutrients for their body to maintain high levels of milk yield, especially during early lactation. Therefore a high dry matter intake (DMI) is very important. A high milk yield will always depend on high DMI as the cows eat more, they will increase their capacity/potential to produce more milk. If the animals do not eat enough they will start to lose body weight and their level of production will be reduced. Low DMI may also result in poor reproductive performance. (www.utextension.utk.edu/publications/pbfiles/pb1598.pdf; 2008-07-01).

Other than the digestibility of diet and the animal´s ability to convert dietary energy efficiently into metabolizable or net energy, DMI is the single most significant variable related to the performance of lactating dairy cows (Mertens, 1994; quoted by Huhtanen, Rinne & Nousiainen, 2007). High yielding dairy cows usually experience a negative energy balance during early lactation because the energy in milk exceeds the energy intake through feed (Reynolds, 2006).

It is difficult, however, to provide sufficient feed to fulfil their requirements for maintenance, production and reproductive growth of the most highly productive dairy cattle. Grass and legume silages are the main forages used in Scandinavia. Grasses and legumes are cut and ensiled at early stages of maturity, when they are highly digestible for feeding to dairy cows. These silages are more important to regulate voluntary feed intake metabolically because, they produce instant metabolites for absorption (Huhtanen, Rinne & Nousiainen, 2007). However high energy requirements cannot be met by feeding only forages, since cows are not able to eat sufficient quantities due to the limited capacity of the reticulo-rumen (Van Soest, 1994). Therefore cereal grains or silages of cereals are usually added to the diets of high productivity dairy cows.

Cereals may affect the rate and extent of rumen fermentation when fed in addition to either to poor quality or good quality silages. Furthermore, the efficiency of metabolizable energy utilization increases as ruminal fermentation shifts towards increased propionate production.

Starch and fibre are the main carbohydrates in the diets of dairy cows. Supplementing diets with starch has become increasingly important in dairy cow productions in recent years. However, one of the drawbacks of starch sources is that they directly interact with ruminal and total tract digestibility of fibre. Starch from barley, wheat and oats is considered to be a rapid rumen degradable starch (Nocek, 1991; Tothi *et al.*, 2003), starch from maize and sorghum is somewhat less rapidly degraded. High quality grass or legume silages (cut at an early stage of maturity) combined with the starch from wheat or barley have been shown to cause a significant decrease in voluntary DMI.

The question is how to avoid the rapid degradation of highly digestible diets in the rumen which is metabolically important for the short term regulation of feed intake. One approach is to combine starch from sources that are degraded slowly with grass or legume silages cut at early maturity. The starch does not undergo

rapid degradation but is digested a little and usually passes through the rumen. Consequently, most part is digested and absorbed in the small intestine.

Another approach could be the processing of sources of starch and combining the product with grass silages cut and ensiled at early maturity. A third approach might be to combine different starch sources with grass silages cut at a variety of stages of maturity. The objective of these approaches is to slow down rumen degradation or to shift the site of starch digestion from the rumen to the small intestine and the hindgut.

The aim of this review is to describe the current state of knowledge pertaining to the physical and metabolic regulation of silage intake in high yielding dairy cows, with special emphasis on the effects of the interaction between fibre and starch in different diets.

3. Digestive anatomy, physiology and regulation of intake in high producing dairy cows

Understanding the anatomy of ruminants and the ecological niche occupied by their rumen is very helpful in grasping the concept of the utilization of forages (Fisher, 2002). The ruminants can be divided into two main groups; concentrate selectors, (*e. g.* goat,) and grass roughage eaters, *e. g.* cattle and buffaloes (Fisher, 2002). Sheep are considered to be intermediate between two types.

The grass roughage eaters have relatively smaller parotid glands, a longer forestomach and a smaller distal fermentation chamber (Figure 1a) in comparison to concentrate selectors (Fisher, 2002). These characteristics make them able to efficiently utilize coarse or fibrous feed (Van Soest, 1994). The alimentary tract of ruminants starts in the buccal cavity with the parotid glands, followed by a long pipe, the oesophagus, a complex stomach consisting of four chambers known as the rumen, reticulum, omasum and abomasum, the small intestine and the long spiral colon (Figure 1a). The total stomach volume in grass roughage eaters occupies three quarters of the abdominal cavity (Van Soest, 1994). The rumen and reticulum are usually treated as a single compartment, the reticulo-rumen forming which is the largest part of the stomach (Figure 1a) occupying 73% of the total volume (Van Soest, 1994) in adult ruminants (*e. g.* cattle). The reticulo-rumen is considered to be the most important fermentation and absorption chamber for coarse or fibrous feed and the contents can move freely between the two chambers (Van Soest, 1994). About 50% of all digestion takes place in the rumen. Finger-like projections, called papillae, in the rumen increase the surface area for the absorption of nutrients after digestion. Reticular ridges in the reticulum help in the sorting and handling of particles before they pass to the omasum. Venous blood is drained from the reticulo-rumen by three veins: the right ruminal, the left ruminal, and the reticular vein. The omasum connects the reticulum to the abomasums (Figure 1 a) and is the main absorptive organ in cattle (30-60% of the total water and 40-69% of total volatile fatty acids (VFA) entering the omasum are absorbed there)(Van Soest, 1994).

The omasum is larger and more active in grass roughage eaters than in concentrate selectors (Van Soest, 1994; Fisher, 2002). Forbes (1995) described the reticulo-omasal orifice as being very sensitive to mechanical stimuli; the opening of this orifice controls the rumen emptying and thus controlling voluntary feed intake and rumination. Ruminants have a population of different microbes that digest cellulytic substances, a system that is absent in non-ruminants. The rumen microbial population includes protozoa, many species of bacteria and some species of fungi. VFA are mainly produced by methanogens and some species of protozoa (Van Soest, 1994). The rate of production and absorption of VFA maintains the balance of the ruminal concentration of VFA. Absorption of VFA into the blood-stream depends on the difference in pH and the concentration gradient between the stomach and the blood. Active transport and diffusion do not seem to be involved in the absorption of VFA as they have been shown to be absorbed in free form against the alkaline pH of blood (Van Soest, 1994).

The abomasum in ruminants functions in a very similar way to the stomach in non-ruminants (Banerjee, 1991): it secretes gastric juice (consisting of HCl, pepsin and mucous) with a pH of 1.0-1.3 which is fatal for microbes and essential for protein digestion. Dietary protein and microbial protein that were not degraded in the rumen are digested here.

A considerable amount of VFA leaves the reticulo-rumen and passes into the abomasum and the duodenum, where it is absorbed. The duodenum in ruminants has two different kinds of chemoreceptors: the first is sensitive to the concentration of potassium chloride and the second is stimulated by VFA (Cottrel & Iggo, 1984; quoted by Forbes, 1995). These chemoreceptors are sensitive to the molecular weights of VFA and not to pH and osmolality. The small intestine has special finger-like structure called villi (which are different from papillae in the rumen) for the absorption of nutrients (Banerjee, 1991).
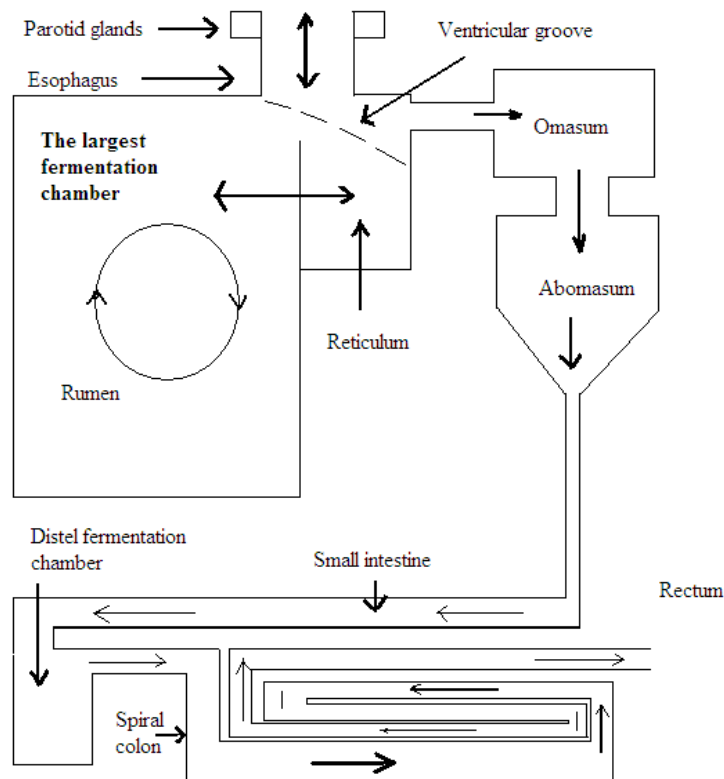
Figure 1a. A diagrammatic representation of a ruminant´s alimentary tract. (After Fisher, 2002)

4. Different theories on the regulation of voluntary intake

The regulation of intake in lactating dairy cows is complex. There is no single factor that could be cosidered the sole regulator of intake, rather it is controlled by a combination of different mechanisms interacting with each other (Fisher, 2002). A single factor can stimulate several types of receptors (Figure 1b) or a single receptor can be stimulated by a number of inputs (Forbes, 1995). In simple terms, it can be divided into short term and long term regulation of feed intake. The events within a day which affect the frequency, size and pattern of meals are considered to represent short term regulation of feed intake, while long term regulation describes the average daily intake over longer periods of production during which maintenance requirements remain the same (Mertens, 1987).
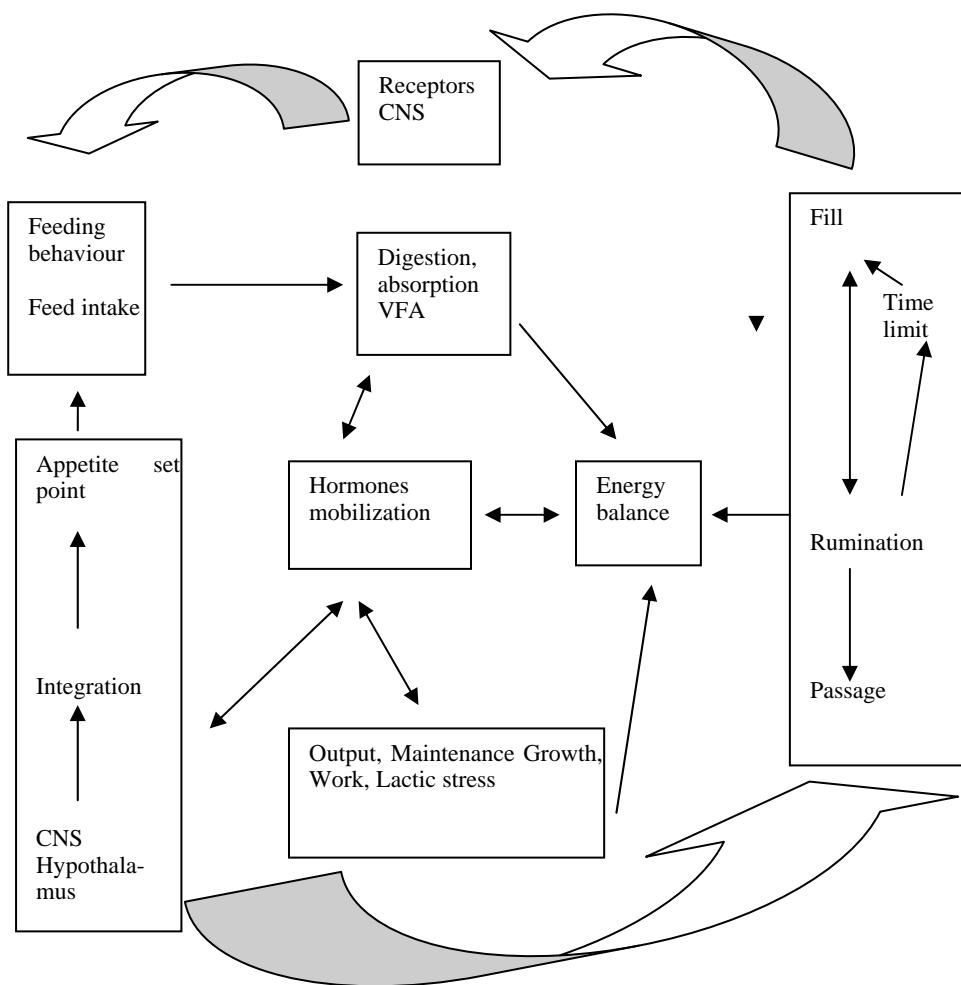
Figure 1b. A schematic representation of the interaction between various factors affecting the regulation of voluntary feed intake. (after Van Soest, 1994)

Feed intake can be limited by the bulkiness of the feed (fill effect) in relation to the volume of the reticulo-rumen (Mertens, 1987; Van Soest, 1994; Allen, 2000; Fisher, 2002); this is the, characteristic of diet that describes the physical regulation of intake. The ruminants' reticulo-rumen volume determines the potential physical intake of forages (Forbes, 1995). The energy content of the diet is the second most influential factor in the regulation of feed intake (Mertens, 1987; Forbes, 1995; Allen, 2000; Fisher, 2002). However, animal body weight (reticulo-rumen capacity), its production potential (energy requirements of high vs. low producers), health status, physiological status (pregnant or non pregnant) and parity (Forbes, 1995) are other characteristics associated with animal´s ability to utilize energy from the diets and which affect feed intake (Mertens, 1987).

Digestion of the feed to produce protein and energy to be used by the animal is a complex process. Many dietary factors are known to influence availability of energy from feed consumed. Fisher (2002) stated that a balance is required between the different dietary components to ensure that the numerous nutritional factors involved in the control of voluntary feed intake are appropriate (Figure 1b).

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A significant decrease in the voluntary intake of DM has been reported when protein is limited or there is an imbalance in the intake of dietary protein. This is probably, due to the metabolic limitations to the processing of energy from carbohydrates in the rumen and the post ruminally (Fisher, 2002). Palatability of diets may sometimes, influences ruminants´ ability to override voluntary intake. Moreover, ambient temperature can affect voluntary feed intake in dairy cows (*e. g.* Forbes, 1995). It has been reported that elevated temperatures decrease DMI and milk production in dairy cows in most tropical areas of the world. All these factors produce some kind of feedback signals via the central nervous system.

Most of the time, metabolic feedback is viewed separately from physical or any other feedback signals, but the central nervous system integrates all of these for the regulation of voluntary feed intake (Figure 1b). Both physical and metabolic short term regulation of intake have been found to be involved when high quality silages are fed to dairy cows (Huhtanen, Rinne & Nousiainen, 2007).

Table 1. *Examples of some dietary factors affecting voluntary DMI*

Dietary factor	Quantification	% increase/decrease in		References
		DMI	Milk yield	
NDF content	35 vs. 25 %	22.4	16.0	Dado & Allen, 1995
	36 vs. 32%	6	ND	Sheperd & Combs, 1998
NDF digestibility	45 vs. 40%	5.1	5.2	Dado & Allen, 1996
	1%	.....	.....	Oba & Allen, 1999b
Glucose infusions	Rumen/duodenum	-5.0	3.0	Boudon *et al.*, 2007
Propionate infusion	Reticulo-rumen	-33.0	.....	Reviewed by Allen, 2000
Acetate infusion	Reticulo-rumen	-14.0	.....	

DMI = Dry Matter Intake
NDF = Neutral Detergent Fibre

5. Physical regulation of intake

The reticulo-rumen represents the first chamber in the alimentary tract of ruminant animals and its capacity sets a limit on the amount that animal can eat (Forbes, 1995). Anything that causes sufficient distension of the reticulo-rumen or any other compartment of the digestive tract triggers the mechanoreceptors, which transmit a message to central nervous system resulting in the cessation of further intake. The idea of physical regulation of feed intake is, essentially, based on the fill effect of diet: eventually fill causes the physical distension of the reticulo-rumen (Mertens, 1987). According to Van Soest (1994), diet composition and physical form have a significant effect on reticulo-rumen fill and passage.

Mertens (1987) discussed whether fill effect of diet on the reticulo-rumen was more important for the short term regulation of intake than the weights of diet. Most theories of intake regulation include the idea that ingestion of feed causes

changes in the body which are monitored by the central nervous system and used to determine when feeding should stop (Forbes, 1995). In dairy cows, physical regulation of intake comes into play mainly when they are fed low caloric and poor quality diets. In such cases, they try to eat more to fulfil their energy and protein requirements based on their production potential (Van Soest, 1994).

Low or poor quality forages (legume/grass) are usually characterised by slower ruminal digestion, longer retention times, delayed clearance from the ruminal compartments and a slow rate of passage, creating dietary fill of the reticulo-rumen (Figure 1a).

The part of the alimentary tract that is most important in the regulation of feed intake by physical fill is the reticulo-rumen (Allen, 2000). Leek and Harding (1975) described how the mechanoreceptors in the epithelial lining of the reticulo-rumen are concentrated in the anterior dorsal portion of the rumen and reticulum (cited by Forbes, 1995). Excitation of these receptors caused by rumen fill causes a message to be sent to the satiety centres of the central nervous system to cease intake (Allen, 2000). Distension in the rumen is determined by both the weight and volume of the digesta. Physical fill can be described on the basis of three main aspects (Figure 2): the reticulo-rumen volume which is mostly related to the animal´s characteristics; the rate of digestion of feed; and the rate of passage (rumen emptying). Improved voluntary feed intake is positively related to ruminal digestibility and the

Physical fill

Reticulo-rumen volume

Rate of passage of feed

Rate of digestion of feed
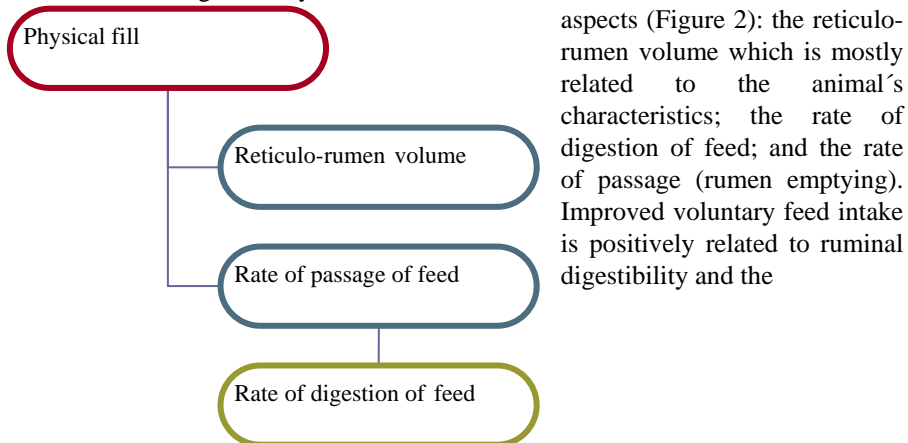
Figure 2. Different animal and feed aspects describing physical fill

rate of passage from the rumen, and negatively related to the fill effect of diets (Van Soest, 1994; Forbes, 1995; Allen, 2000). Grass forages with a high ruminal rate of digestion have been associated with increased voluntary feed intake, since the faster rate of digestion results in the reticulo-rumen emptying more quickly. Although ruminal digestion of neutral detergent fibre (NDF) and organic matter (OM) in legume or whole crop silages is lower than in the grass silages, the total DM intake is high for the former. This phenomenon supports the established fact that legume or whole crop silages exhibit the faster rates of passage. Van Soest (1994) suggested that the additional intake of feed becomes possible once the reticulo-rumen is cleared.

5.1 Physical capacity of the rumen (rumen volume)

There is a positive correlation between the physical capacity of the rumen and feed intake. Not only is feed intake affected by digestibility (the rate and extent of degradation) and passage rate but also by the capacity of the digestive tract, principally the rumen (Forbes, 1995). A positive correlation has been found between the level of intake and the weight of the empty reticulo-rumen in lambs (Wardrop, 1960; quoted by Forbes, 1995). There is also a positive correlation between feed intake and body size (with a standard fat content) in mature and growing animals. In contrast, a negative correlation (Table 2) is found between feed intake and body capacity for fatty animals (Forbes, 1995). The possible explanation for this negative relationship is that abdominal fat reduces the capacity/volume of the reticulo-rumen (Table 2), as has been observed in pregnant animals in the last trimester of pregnancy. Heifers in the last 14 weeks of pregnancy reduced intake of a complete feed by 1.53% per week with an even higher rate of decline in the last two weeks (Forbes, 1995).

Ingvartsen, Andersen & Foldager (1992) showed that changes in voluntary intake in late pregnancy ranged from an increase of 0.2% per week to a decline of 9.4% per week. Cows in late pregnancy ate less hay than non-pregnant cows (Campling, 1966) and voluntary intake has been seen to decrease during the last month of pregnancy (Owen, Miller & Bridge, 1968). A correlation has been found between the reduction in DMI in the last six weeks of pregnancy and the birth weight of the calf (Lenkeit *et al.*, 1966). All these studies suggest that the decrease in DMI is due to there being less available space in the rumen of pregnant animals (physical capacity of rumen is reduced as a result of increasing foetus size) (reviewed by Forbes, 1995).

Table 2. *Factors affecting the capacity of the reticulo-rumen*

Factor	Effect	References
Body fat	Decreases	Forbes, 1995
Pregnancy	Decreases	Forbes, 1995
Inert fill	Decreases with high fibre diets	Dado & Allen, 1995
Diet NDF	Decreases with increased feed intake	Van Soest, 1994

NDF = Neutral Detergent Fibre

5.2 Water content of feeds (rumen volume)

There is a decrease in the DMI of silages as the water content increases. Balch & Campling (1961) conducted a series of experiments to describe this phenomenon and reported that there was a 0.54 kg /day decrease in DMI for each 10 L of water when balloons filled with 50-100 L of water were introduced into the rumen of non lactating, non–pregnant mature cows (quoted by Forbes, 1995). Water-filled balloons were assumed to behave just like water in stems and leaves causing inert fill. High moisture content in silages produces water filling effects the in rumen because the contents of the cell are digested and cells with a cell wall behave like water-filled ballons, producing the sense of rumen fill (Hotel Theory by Van Soest,

1994). High moisture content of forages increases the bulkiness of diets and is negatively related to capacity of the reticulo-rumen.

5.3 Reticulo-rumen motility (rate of passage)

Increased motility, as occurduring feeding, increases the rate of outflow of digesta from the rumen (clearance of reticulo-rumen) leading to decreased distension and, potentially, to increased DM intake (Forbes, 1995). Increased motility of the reticulo-rumen also produces more contractions that send feed to the buccal cavity for rumination causing particle size to be reduced and passage rate to increase, eventually increasing feed intake. High concentrations of VFA have been reported to reduce reticulo-rumen motility (Forbes, 1995) having a negative impact on the digestibility of NDF. This can be explained by the effect of VFA concentrations on ruminal pH. High concentrations of VFA also have an impact on rumination and thus on particle reduction, eventually slowing down the rate of passage and rumen emptying.

5.4 Fill effect of diets (rumen volume)

Fibre or cell walls can be defined as the fraction of any feed that is slowly or incompletely digested. NDF, the neutral detergent insoluble fibre, consists of cellulose, hemicellulose and lignin. Rumen volume is greatly affected by the NDF content of forages (Van Soest, 1994). The NDF content is inversely related to the digestibility or energy density of the feed.

Forage NDF in diets can inhibit feed intake, as a result of rumen fill, when it exceeds a maximum threshold; it has been directly related to the fill effect of the diet (Mertens, 1987) as a result of its bulky nature. A proportional increase in forage in diets decrease voluntary DMI (Dado, 1995) and diets with high forage content usually exhibit lower rumen digestibility. Obviously such diets spend longer time in the rumen, pass through slowly, create more distension and thus reduced intake.

Dado & Allen (1995) observed that cows produced 5.2 kg/day more milk and consumed 5.1 kg/day more DM when fed low fibre diets (25% NDF) compared with high fibre diets (35% NDF of dietary DM) when the diets were equal in nutrients composition with respect to crude protein, OM *etc*. Apparent total tract digestibility and fractional passage rate were higher for DM, OM, NDF and lignin for diets with a low NDF content (Dado, 1995). This is the reason that there is high DMI with low fibre diets. Sheperd & Combs (1998) reported an increase of approximately 6% in voluntary DMI (25.7kg/day vs. 26.3kg/day) when comparing dairy cows fed diets with high forage (35.9%) and low forage (31.8%) respectively. The study was undertaken to investigate the effects of the infusion of acetate and propionate and their long term effects with high and low fibre diets. The consumption of DM was 2.75% and 3.25% of body weight for high and low forage diets, respectively. Nelson *et al.* (1968) concluded that there was a linear decrease in DMI (from 3.18 to 2.67%) as a percentage of body weight when the forage inclusion level was increased from 0 to 100% of the diet.

5.5 Feeding behaviour associated with high NDF diets

Feeding, chewing and ruminating behaviours have been shown to change greatly in relation to the inclusion level of forage in the diets. In general, cows spend more time chewing and ruminating per unit of DM or NDF intake when diets has a high forage content compared to concentrate or pelleted diets. Dado & Allen (1995) also noted some changes in feeding and chewing behaviours. For example, with increased forage in the diet, a smaller meal size and inter-meal interval was required to maintain the maximum fill level in the cow´s reticulo-rumen; the animals also spent more time chewing per unit of DM or NDF intake, and there were more and longer bouts of rumination (a period of time spent in a particular activity; http://www.thefreedictionary.com/bout   2008-08-16). A positive relationship has been found between the NDF content of diets and rumen fill, and a negative relationship between NDF content and energy density of diets. The best possible combination could be determined for different ingredients on the basis of NDF content in the diet (Mertens, 1987; Dado & Allen, 1996).

5.6 NDF digestibility (rate of passage)

Neutral detergent fibre digestibility (NDFD) could be related to the rate of digestion of forages in the reticulo-rumen. Forage NDFD is an important parameter for determining forage quality, in addition to other factors such as NDF content, maturity stage and source (grasses or legumes). NDFD is perhaps more important when it is related to DMI, production and feeding behaviour in dairy cows (Oba & Allen, 1999).

Dado & Allen (1996) conducted an experiment to determine the effect of NDFD of the alfalfa silages on DMI and milk production. They offered two silages of alfalfa with the same NDF content (40%) but different NDF *in vitro* digestibility (a technique used to measure the degradability of different ingredients e.g. DM, OM, NDF etc. in laboratory using rumen fluid and a buffer solution). The two silages contained 40% and 45% high and low *in vitro* digestible fibre respectively. They found increased milk yield (36.3kg/day vs. 38.2kg/day) and DMI (19.4kg/day vs. 20.4kg/day) for the highly digestible and poorly digestible fibre diets, respectively. The net effect on DMI and milk yield was 1.0kg/day and 1.9kg/day, respectively. The mean total tract digestibilities of DM, OM and NDF were 4.2% higher for all nutrients in the diet with more digestible fibre (Dado, 1996).

Forage fibre digestibility may also influence feed intake, especially if feed intake is limited by the physical capacity of the reticulo-rumen (Dado & Allen, 1996). Oba & Allen (1999b) reported that forages with high NDFD resulted in higher DMI, milk yield and 4% fat corrected milk yield and body weight gain when they compared forages belonging to different families (among grasses, among legumes and between grasses and legumes).

Forages with high NDFD might increase DMI when physical fill limitations to feed intake exist (Oba & Allen, 1999). A one unit increase in forage NDFD *in vitro* or in situ has been associated with a 0.17kg/day increase in DMI, a 0.23kg/day increase in milk yield and a 0.25 kg/day increase in 4% fat corrected milk yield (Oba & Allen, 1999). *In situ* analysis is a similar technique to *in vivo,*

with the difference that it uses feed contained in small bags; it has proved very useful for fractional rate of passage studies in live animals). A linear relationship between the marginal increase in the digestibility of NDF and animal performance was also found (Oba & Allen, 1999).

Many *in vitro* studies to determine the OM and NDF degradability of different feed stuffs (*e. g.* Hetta *et al.,* 2007) have shown a greater silage intake when there is higher *in vitro* NDF degradability. A positive correlation has been found between the *in vitro* NDF degradability of silage and silage dry matter intake.

Brown mid-rib corn is characterized by a brown pigmentation in the leaf midrib (http://agguide.agronomy.psu.edu/cm/sec4/sec42f.cfm; 2008-06-26). Cell walls of brown mid-rib corn are proportionally less lignified than normal corn varieties (almost half the normal amount). A gene (*bm3*) is responsible for the reduced lignin content. Brown mid-rib plants exhibit a 6-8% increase in total plant digestibility. Several studies on the performance of lactating dairy cows fed on brown mid-rib corn silage vs. normal have found a significant increase in DMI (about 10%) and milk yield simply as result of the high *in vitro* degradability of the NDF (Oba & Allen, 1999a;b).

6. Metabolic regulation of intake

The VFA produced by rumen microbes represents up to 70 % of the energy supply to the animal. The VFA are produced as a result of rumen microbial degradation of feed and are transported into the blood stream via the hepatic portal vein. VFA are the main energy carrying molecules in the blood stream, representing the energy status of the body of ruminants as glucose does in non ruminants. When the energy or protein needs of dairy cows are fully supplied by the feed, then further intake is reduced as a result feedback via the satiety centre of the central nervous system. Boudon *et al*. (2007) suggested that the amount of energy absorbed in the form VFA could be a strong limitation to voluntary intake. Apparently, diets containing high levels of concentrate or high quality silages have been found to depress feed intake (Forbes, 1995; Allen, 2000). The mechanism involved is the production of high concentrations of VFA over a very short period of time, due to the high rate of rumen digestion; these are absorbed readily into the blood-stream. Consequently, this increased level of VFA or energy entering the blood-stream depresses feed intake (Forbes, 1995; Allen, 2000).

The main area sensitive to metabolic regulation of intake in the digestive tract of ruminants is the reticulo-rumen, probably because it has epithelial receptors for detecting the products of rumen metabolism *e. g*. VFA. The excitation of these receptors produces a feedback to the central nervous system (Figure 1b) and as a result further intake of feed stops (Forbes, 1995). The excitation of epithelial receptors is considered to be due to the titratability of the acids in question, which has a negative impact on reticulo-rumen motility (Forbes, 1995). As more VFA is produced, the concentration of acids in the rumen increases and ruminal pH decreases until it reaches a plateau at which VFA concentration is still high (Forbes, 1995). At this pH the activity of reticulo-rumen muscles is affected, thus

reducing the reticulo-rumen motility which in turn reduces rumination and the rate of the passage of feed. When ruminal pH falls below 5.0, rumen stasis occurs and further depression of feed intake may be due to rumen stasis and not due to lower ruminal pH (Forbes, 1995).

Forbes (1995) quotes Bhattacharya & Warner, (1967) who infused various acids into the rumen but maintained a pH of 6.0. There was a reduction in DMI due to the inhibitory effect of acidity on reticulo-rumen motility, not as a result of lower pH. Reduced DMI associated with silages in comparison to hay is more likely to be due to acid production during ensiling and the consequent effects on rumen muscular activity rather than on rumen pH (Forbes, 1995).

The areas other than reticulo-rumen that play a role in the control of metabolic regulation of intake are the liver and the small intestine. Chemoreceptors for VFA concentration are found in the liver (Allen, 2000), they are especially sensitive to the propionate concentration of the blood (Anil & Forbes, 1980). It is obvious from different studies (*e. g.* Boudon *et al.*, 2007) that the receptors occupying the epithelial lining of the duodenum are also sensitive VFA concentrations.

6.1 Volatile fatty acids

It has been reported that high quality silages (with faster ruminal digestion of soluble carbohydrates and fibre) produce high levels of VFA in the reticulo-rumen (*e. g.* Hetta *et al.* 2007; Huhtanen, Rinne & Nousiainen, 2007). These VFA can affect voluntary feed intake in three different ways: 1) they affect rumen pH thus reducing NDFD; 2) they affect the tonicity of the epithelial muscles and slow down reticulo-rumen motility, resulting in decreased bouts of rumination and a decreased rate of passage of feed (both related to reticulo-rumen fill); 3) they regulate intake by metabolic means after absorption into the blood-stream (Forbes, 1995). It has been reported many times that infusion of VFA reduces feed intake (Baile & Forbes, 1974; De Jong, 1986; quoted by Forbes, 1995) and that it should be regarded as supplying external energy (Sheperd & Combs, 1998) in addition to the energy from the diet.

Faverdin (1990) showed that 3 or 6 mol of a mixed solution of VFA infused into the rumen during three hours of feeding depressed DMI by 1.5 kg in lactating cows. However it depressed DMI only by 0.8 kg in dry cows. There is a significant relationship between infusion of VFA and depression of DM intake in the range 2.5-20 mmol /min in goats (Baile & Mayer, 1969). Forbes (1995) suggested that the main effect on DMI was due to the propionate and acetate in the mixture of acids. The epithelial receptors of reticulo-rumen might act as chemoreceptors. Leek (1986) questioned whether epithelial receptors have a physiological role as chemoreceptors in view of the high concentration of chemicals required to activate them and their long response time (quoted by Forbes, 1995).

6.2 Propionate versus acetate

Propionate is the most important of all VFA for the metabolic regulation of voluntary feed intake (Forbes, 1995). The chemoreceptors for propionate are located in the liver (Allen, 2000). Infusion of VFA, particularly propionic acid or

sodium propionate, into the portal vein reduces DMI. Choi & Allen (1999) reported that propionate in the form of either Na propionate or propionic acid, infused into the reticulo-rumen of dairy cows, reduced meal size and meal length more than did NaCl or Na acetate infusions (Choi & Allen, 1999; Allen, 2000). The addition of propionate reduced DMI more than the addition of acetate when infused in isocaloric amounts, over a longer period of time, in dairy cows (Sheperd & Combs, 1998; Allen, 2000).

Anil & Forbes (1980) reported that there was a marked reduction in intake (about 80%) after the injection of propionate in the portal vein of sheep, whilst there was little or no effect on intake when infused into the jugular vein. However, when high forage diets were fed to lactating dairy cows, high levels of acetate in the mixture of acids could be a factor in regulating intake (Sheperd & Combs, 1998). The infusion of propionate into the reticulo-rumen decreased DMI more than the infusion of acetate: almost 14% and 33% for acetate and propionate respectively when compared to control feeding (reviewed by Allen, 2000).

In a study conducted by Sheperd & Combs (1998), voluntary DMIs were 24.9kg/day and 23.5kg/day with the continuous infusion of acetate and propionate with high fibre diets. The cows, on average consumed 3.47% and 3.32% of their body weight as DM, and propionate had a greater inhibitory effect than acetate.

The possible decrease in intake associated with propionate is probably due to more insulin secretion into the blood as suggested by Grovum (1995). Propionate infusions are more important because they increase plasma insulin, and increased secretion of insulin in plasma results in decreased DMI in sheep (Foster, Ames & Emery, 1991). Furthermore propionate concentrations in the pancreas would be higher and more likely to stimulate insulin secretions when infused into the portal vein than when injected into the jugular vein (reviewed by Allen, 2000). Infusions of a mixture of VFA into the reticulo-rumen decreased DMI for lactating cows but had little effect on DMI for dry cows (Farningham & Whyte, 1993).

The effect of intraportal infusions of propionate is not consistent and varied from animal to animal and from experiment to experiment, and therefore cannot be generalised (reviewed by Allen, 2000).

6.3 Glucose versus VFA

Glucose is not the main energy-yielding substrate for maintaining the body energy balance in ruminants and is found in relatively small concentrations in the blood plasma when compared to non-ruminants (Forbes, 1995). Although it does play a key role in many functions such as brain metabolism, nourishment of the foetus and milk synthesis (Banerjee, 1991). Glucose is generally regarded as the least significant metabolic regulator of voluntary intake in ruminants. Glucose is significant for the voluntary control of DMI in non-ruminants but not in ruminants (e. g. Allen, 2000). Non-ruminants (*e. g.* pigs) are only able to convert starch into its metabolizable products (maltose and glucose), so glucose is their primary energy yielding substrate (Banerjee, 1991). Faverdin, Richou & Peyraud (1992) showed that a mixture of VFA (64%, 21% and 15% of acetate, propionate and butyric acid respectively) comprising 20.3 MJ/day of metabolizable energy infused

into reticulo-rumen decreased DMI by 12% but no effect was observed with the infusion of isoenergetic glucose solution into the abomasum.

In some other studies glucose infusions into the rumen or into the duodenum have been shown to produce negative effects on DMI. Boudon *et al.* (2007) conducted an experiment to determine whether total energy intake could limit DMI and whether the limitations on DMI were specific to the site of energy absorbed and its subsequent effects on DMI, milk yield and feeding behaviour in lactating dairy cows. The cows were fed fresh ryegrass *ad libitum* with the following treatments: 1) infusion of 1.25 kg of glucose into the rumen; 2) infusion of 2.5 kg of glucose into the rumen; 3) infusion of 1.5 kg of glucose into the duodenum; and 4) a control treatment consisting of infusion of water and salt. The results showed an average decrease of 0.95 kg/day and 3.4 kg/day DMI and as fed intake for the ruminal or duodenal infusions, respectively. No significant difference was found between the site and dose rates of glucose infusions. Milk yield increased by 0.8 kg/day but milk fat content tended to be lower and the effect was more significant with duodenal compared to ruminal infusions (Boudon *et al.*, 2007).

Reynolds (2006) quoted Rigout *et al.*, (2003), who summarized a number of studies and analysed the data from these. A linear increase in milk yield (2.5 kg/day at 29.3 MJ/d), milk protein yield (0.3% at 54.4 MJ/d) and a curvilinear decrease in milk fat content (1.4% units at 54.4 MJ/d) was reported when glucose was infused into either the duodenum or the abomasum.

7. The role of fibre and starch and their interaction (level and quality of fibre and starch) in the control of voluntary feed intake

Carbohydrates such as fibre and starch are the main source of energy in the diets of ruminants and VFA are the major energy yielding substrates (Anil & Forbes, 1980; Nocek, 1991). Carbohydrates provide energy for body activities, microbial activity, they provide carbon skeleton for microbial protein synthesis, and they are necessary for normal rumen functioning. Rumen microbes can utilize carbohydrates or secondary products for growth and activity (Nocek, 1991). Amino acids and fatty acids can also be utilized for these activities but less efficiently.

The behaviour of carbohydrate digestion differs between the rumen and the postrumen section of alimentary canal, not only with the respect to type of carbohydrate (fibre or starch) but also the origin and amount consumed by cows (Nocek, 1991). Carbohydrates can be divided into two broad classes; structural and non-structural carbohydrates (NSC). Structural carbohydrates are mainly found in the cell walls. Cell wall constituents include polysaccharides (structural carbohydrates), hydrocinnamic acids, lignin, and proteins, and also called fibre (Van Soest, 1965). The NDF could be defined as the portion of cell wall which is neutral detergent insoluble and consists of cellulose, hemicelluloses and lignin. The fibre portion makes up 300 to 800 µg/g of forage DM (Hatfield, Ralph &

Grabber, 1999). Cellulose is the most important structural carbohydrate. It is required for normal rumen functioning (Banerjee, 1991; Van Soest, 1994) and ruminants are able to convert it to valuable products such as meat and milk (Jouany, Michalet-Doreau & Doreau, 2000). Cllulose is a polysaccharide, in which glucose monomers are linked together through a beta 1-4 glucosidic linkage.

7.1.1 Factors important for cell wall (fibre digestion)

Forages (grasses and legumes *etc.*) play an important role in ruminants' feeding because they are slowly digested in the rumen and provide nutritional energy. Although one unit of forage DM contains almost the same amount of gross energy as one unit of cereal grain DM (Ralph *et al.*, 2004), the energy provided to the animal is comparatively lower. It can be much lower and varies in the range of approximately 33% (wheat straw) to 70% (silage maize) or 80% (leafy rye-grass) that of maize grain. This lower energy value for forages is attributed to the presence of cell wall (fibre) and its limited digestion in the rumen. According to Hatfield, Ralph & Grabber, (1999) and Ralph *et al.*, (2004) the cell walls are the controlling factors in determining the quality of forages and, in most cases, less than 50% are digested (*e. g.* forage maize).

Furthermore, the composition and organization of the cell wall components determine its role as a structural and functional unit. Among the cell wall components, lignin is the major culprit in imposing limitations on the degradability of the cell wall. Lignin is that fraction of fibre, which gives structural integrity and hydrophobicity to the plant cell wall, and is almost completely resistant to degradation. Lignin, with its variable structure, and its cross linkage involving polysaccharides and hydroxycinnamic acids (Ralph *et al.*, 2004) is difficult for rumen microbes to utilise.

7.1.2 Fibre digestion is affected by the stage of maturity of forages

Forage fibre digestion is affected by their stage of maturity because chemical composition changes with crop age. Forage NDF replaces soluble sugars as the plant matures. It has been shown in different studies (Hatfield, Ralph & Grabber, 1999; Ralph *et al.*, 2004) that lignification of cell walls increases as grasses become older and this affects the rate of digestion and digestibility of NDF in grass silages. Rinne, Huhtanen & Jaakkola (1997a) studied the effects of maturity of Timothy grass (*Phleum pratense* L.) silage fed to dairy cows. They concluded that grasses cut at four different maturity stages (at one week intervals) with 40.9, 48.1, 57.9 and 62.5% NDF content form youngest to oldest had total tract digestibilities of 75.7, 76.5, 69.2 and 68.6% respectively. Collectively, a decrease of 0.25% in diet NDFD for each additional day's delay during the harvest season has been found (Rinne, Huhtanen & Jaakkola, 1997b).

In addition to the characteristics of the ruminant, NDFD is also dependent on the type of plant and environmental factors. Experiments conducted on Timothy grass to investigate the effects of seasonal variation on biochemical composition and digestibility, showed an approximate decrease of 1.28% for each additional day 's delay (see Table 5) in *in vitro* digestibility of OM (Gustavsson & Martinsson, 2004). The grass was harvested at different maturity stages over 101 days period

during the years of 1995 and 1996 and NDF content increased at the rate of approximately 2.12 g for each day that harvest was delayed.

In another study (Bernes, Hetta & Martinsson, 2008), the *in vitro* degradability of NDF has been shown to amount to 89.4, 85.2 and 77.8% for early (16 June), mid (20 June) and late (26 June) cuts of Timothy grass (*Phleum pratense* L.) at the first harvest. The degradability of NDF decreased by 11% over a period of only 10 days as a result of the increased proportion of stems in relation to leaves comprising the whole plants.

Jensen *et al*. (2005) studied the effects of the maturity of maize silage for three different maturity stages and reported 56.0, 51.0 and 43.0% total tract NDF digestibility for early, mid and late cut maize silages in 2000. Interestingly, the total DM intake was increased from 15.2 kg/day to 15.9 kg/day with maximum intake of 16.7 kg/day for the mid-cut silage.

7.1.3 Fibre digestion is affected by starch in the diet

Ruminal fibre digestion is greatly affected by the amount of starch available and how muchof it is digested in the rumen. Ruminal and total tract fibre digestion is usually depressed with increasing amounts of starch in the diet; increased degradation of starch in the rumen is associated with decreased fibre digestion. Lower ruminal digestion of fibre was found in associated with starch from wheat, barley and oats than that from maize and sorghum.

Martin, Philippeau & Michalet-Doreau (1999) demonstrated different ruminal fibre digestibilities (49.4% vs. 57.3%) for diets containing wheat and a flint variety of maize, respectively. The ruminal digestibility of fibre was 16% greater for the diets containig maize. In general, a 8.7% decrease in fibre digestion was recorded when the amount of starch in the diet increased from 30% to 60% (Poncet *et al.*, 1995; quoted by Jouany, 2000).

It has been shown in different studies (*e. g.* Yang, Beauchemin & Rode, 2001) that processing cereal grains, with the intention of increasing starch digestion in the rumen, decreases NDF digestion therein. There was a 3% decrease in NDF digestion for a 32% increase in starch digestion in the rumen for coarse vs. rolled barley grains. In another study conducted by Beauchemin, Yang & Rode, (2001) medium flat temper rolling of barley grains resulted in a 4% decrease of total tract digestibility of fibre compared to unprocessed grains.

Moreover, Shabi *et al.* (1999) reported how the type of processing and frequency of feeding could affect the NDF digestibility. Extrusion vs. grinding of corn and twice daily feeding increased ruminal NDF digestibility by 24% but the same type of processing with feeding four times a day had no effect on rumen digestibility; although total tract digestibility of NDF was decreased by 12% (Table 6).

On the other hand, NSCs are often water soluble (*e. g.* Pectin and most of the sugars), the exception starch, which is insoluble in water. Starch forms 70-80% of total NSC in the cereal grains (Nocek, 1991). NSC is usually degraded rapidly and almost completely in the rumen. Starch is a polymer of glucose monomers and consists of two major molecules; amylose and amylopectin. Amylose contains only

alpha 1-4 D glucosidic linkages between the glucose monomers but amylopectin also contains branches that are linked in straight chains by alpha 1-6 D-glucosidic linkages.

The two major molecules (amylose and amylopectin) are linked together by hydrogen bonding (Nocek, 1991). Starch granules are insoluble in cold water and swell reversibly; in addition, they have non-organised amorphous areas where water can move freely and pseudo-crystalline regions which offer resistance to water infiltration (Nocek, 1991).

As the milk yield from highly productive lactating dairy cows increases, their metabolizable energy (glucose) requirements also increase, so concentrates, usually from cereal grains, are provided in addition to forage (grass/legume) in order to provide more fat or starch. Starch is normally added to increase energy density and to meet the glucose requirements of high yielding dairy cows (Reynolds, 2006). Starch is directly hydrolysed to glucose and provides an instant source of metabolizable energy for the synthesis of milk. Starch is a appropriate source for the supply of precursor of glucose; the propionate, in the rumen, and is an important source of glucose in the small intestine (Reynolds, 2006). In small intestine, glucose derived from starch, is directly absorbed for the synthesis of milk lactose. Starch derived from cereal grains can be metabolisedsmore efficiently to produce energy than cellulose derived from forages. This is because, starch can be transformed into glucose in two steps, while the process of transforming cellulose into glucose is very complex:

In the rumen: Cellulose (crystalline) $\longrightarrow$ Cellulose (non-crystalline) $\longrightarrow$ Cellobiose $\longrightarrow$ D-Glucose $\longrightarrow$ Fermentation (VFA)

In the small intestine: Starch $\longrightarrow$ Amylose/amylopectin $\longrightarrow$ D-glucose

7.2.1 Factors important for starch digestion

Reynolds (2006) described how fibre digestion and DMI were affected by the starch type, frequency of feeding, degree of processing of the feed, the type of fibre fed and the availability of nitrogen for the synthesis of microbial protein.

When starch from barley or wheat (Table 3) is provided, there is a decrease in DMI, so highly rumen degradable starch sources depress fibre degradation by affecting pH, increase the fill effect of the diet (physical regulation of intake) and enhance production of propionate which is a potential suppressor of voluntary intake, *i. e.* metabolic regulation of intake (Tothi *et al.*, 2003; Reynolds, 2006).

Different sources of starch are associated with different rumen degradability. Starch from wheat and barley exhibits rapid rumen degradation but starch from corn or sorghum it is comparatively stable (Reynolds, 2006). Starch digestibility and its effects on DMI, milk yield and milk composition could be different for different sources of forage fibre fed, for example, when ensiled forages are substituted for forage hay. In a review of studies (Theurer *et al.* 1999; quoted by

Reynolds, 2006) it was suggested that rumen degradability, total tract digestibility and DMI were not altered when starch from ground barley was substituted for corn meal, steam flaked corn or sorghum grains along with alfalfa hay, or cotton seed hulls, although these combinations were usually intended to increase DMI and fibre digestion.

Jensen *et al.* (2005) concluded that the stage of maturity of maize silages could affect starch rumen and total tract digestibility. Starch digestibilities were 99% and 98% for mid and late cut maize silages if the digestibility for early cut was assumed to be 100% (Jensen *et al.*, 2005).

Starch digestibility in the gastro-intestinal tract is mainly affected by the type and degree of processing. Nocek (1991) described the important factors influencing starch digestion and its post-ruminal delivery; these are the type and amount of carbohydrate fed, grain processing, particle size reduction and particle passage rate. Starch granules exhibit reversible swelling if they are heated at a lower temperature (55°C) in the presence of water. If, however, they are heated at temperatures between 60 to 80°C or more, they undergo irreversible changes and become gelatinised (Nocek, 1991). However, temporary changes can be reversed by cooling and drying. During gelatinization, the crystallinity of granules is affected and they are ruptured completely by a combination of heat, moisture, pressure and mechanical sheer force (Nocek, 1991).

Physical processing of grains includes breaking, cracking, grinding and rolling of dried grains. Usually physical processing is more useful than chemical processing, and it increased the amylolytic digestion by both microbial and pancreatic enzyme action (Nocek, 1991). However, chemical processing could increase or decrease ruminal digestion depending on the treatment and the type of chemicals used. Physiochemical processing of grains converts the starch granules into hydrated crystalline and amorphous structures, and thus allowing them to separate from the protein matrix of the endosperm and exposing them to more enzymatic digestion (Nocek, 1991). Several chemicals (*e.g.* NaOH, formaldehyde *etc.*) can be used to increase or decrease digestibility of starch in the rumen or the entire digestive tract. In one study quoted by Nocek (1991) formaldehyde treatment of corn decreased ruminal starch digestion by 38%, but it increased in the small intestine so that total tract digestibility remained unaffected.

7.2.2 Starch infusions

Starch infusions are usually thought to affect DMI in a negative way in lactating dairy cows. Starch from different cereal sources can be infused to measure the amount utilized in the rumen and post-ruminally. However propionate production and absorption increased when there is infusion of starch into the rumen (Reynolds, 2006).

Reynolds *et al.* (2001) infused different levels of purified maize starch (0, 700, 1400, and 2100 g/day) into the duodenum of dairy cows and found little or no effect on total DM intake (18.0 kg/day vs. 18.3 kg/day) but milk yield increased from 31.8 kg/day to 33.1 kg/day linearly for infusions vs. control; in addition, there was a decrease in milk fat content.

7.2.3 Appropriate site for the digestion of starch

Most of starch digestion takes place in the rumen. However, excessive starch digestion in the rumen is best avoided in order to reduce the chances of lactic acidosis occuring. According to the results of many studies (Nocek, 1991; Reynolds *et al.*, 2001; Tothi *et al.*, 2003) the appropriate site for the digestion of starch is the small intestine where it is converted to glucose and absorbed for the direct synthesis of milk. When it is digested in the rumen, it is absorbed in the form of propionate, which is converted to glucose in the liver (Reynolds, 2006).
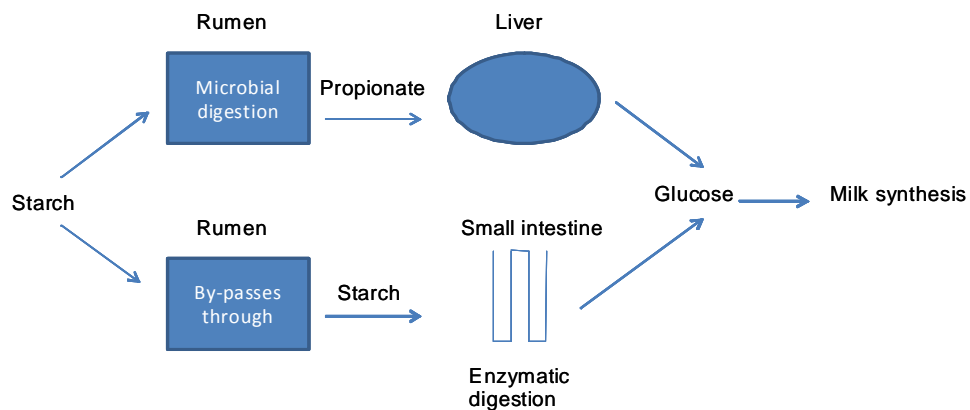
Figure 3. A schematic representation of starch metabolism in ruminants

The site of starch digestion (Figure 3) determines the amount and nature of energy available to dairy cows. Metabolizable energy would be supplied mainly: through the absorption of VFA if starch is digested in the rumen; and mainly through the absorption of glucose if it is digested in the small intestine and hindgut (Reynolds, 2006). Liver glucose production is increased by the infusion of starch into the rumen, while portal vein absorption of glucose is increased by the infusion of starch into the abomasum (Reynolds, 2006). The shifting of the site of starch digestion from the rumen to the small intestine enhances starch digestion and availability of energy for the milk production (Nocek, 1991). Therefore, it is preferable that starch digestion occurs in the small intestine, as this will increase the availability to the animal of glucogenic (propionate *etc.*) precursors (Svihus & Taugbol, 2006).

Table 3. *Ruminal degradation of starch (in %) from different feed sources*

Starch source	Rumen degradation
WeiPass@ (*Triticum aesivum* L.)[1]	80
Sodium Hydroxide treated wheat (*Triticum aesivum* L.)[1]	60
Ground wheat (*Triticum aesivum* L.)[1]	90
Field beans (*Vicia faba* L.)[2]	65
Barley (*Hordeum vulgare* L.)[2]	89
Maize (*Zea mays* L.)[2]	50

[1]Results from Hvelplund *et al*., 2008
[2]Based on a combination of data from Mills *et al*., (1999) and Nocek & Tamminga (1991)

7.2.4 Post ruminal starch digestion:

Starch digested post ruminally (in the small intestine and hindgut) accounted for different proportions of total NSC in different studies (Appendix Table II). According to Owens, Zinn & Kim (1986) between 47 and 88% of the total starch entering the small intestine is digested. Reynolds (2006) described an experiment on the digestion of starch conducted by Knowlton *et al.*, (1998); for every kilogram of starch entering the small intestine, 695g was digested, but in hindgut only 368g/kg was digested (Reynolds, 2006). In another study starch digestion of total the NSC entering the small intestine and hindgut were shown to be 622g/kg and 111g/kg respectively (Abramson *et al.*, 2005; quoted by Reynolds, 2006).

The maximal starch digestibility in the small intestine was recorded as 810g/kg of total NSC cited by Reynolds (2006). At a duodenal flow of 4kg/day of NSC, the amount of starch digested was 3.4kg/day when 1.5kg of maize starch was infused into the abomasum (Arieli *et al.*, 2001). NSC digestion post-ruminally was shown to be 811 g/kg and 746 g/kg of NSC flow to the duodenum for extruded vs. ground corn fed twice daily (Shabi *et al.*, 1999). Starch digestion in the hindgut has been recorded in the range 33-62% of the total entering (Owens, Zinn & Kim, 1986). Physical starch structure, enzyme capacity of the small intestine, glucose absorption and protein flow or infusion to the small intestine were the factors that can affect starch digestion in the small intestine (Reynolds, 2006).

The site of starch digestion can alter the net absorption of energy in the form of VFA and glucose (Reynolds, 2006). Enhanced supply and digestion of starch in the small intestine enhances glucose supply for the synthesis of lactose, in addition the milk yield increases and there is a decrease in milk fat content and total milk fat yield. Thus there is a small difference in net energy yield through milk (Reynolds, 2006; Boudon *et al.*, 2007). Starch digestion in the small intestine is valuable but it cannot be increased to more than 70% of the total entering due to limited production of endogenous enzymes in the small intestine. It is clear from the experiment (Hvelplund, 2008) that processing grains and legumes, which decreased starch digestion in the rumen, could not compensate the total tract digestibility of starch.

7.3 Production responses for the site of carbohydrate digestion

There is a hypothesis that the site of starch digestion could affect production performance of lactating dairy cows. Several studies on the performance of growing cattle have demonstrated the fact that starch is utilized 42% more efficiently if it is digested in the small intestine rather than in the rumen (Owens, Zinn & Kim, 1986).

8. Feeding behaviour

Studies on change in feeding behaviour as a result of different diets fed to dairy cows provide a good picture of feed intake. Feeding behaviour is a combination of short term and long term activities eating feed, chewing, ruminating and drinking over a 24 hours period. Diets with different ingredient and thus different processing methods can alter the short and long term responses of cows. For

example, an increase in chewing and ruminating time has been recorded for diets with a high fibre content. Increasing the amount of unsaturated fats in diets linearly decreased meal size by 0.22 kg DM/meal. However, increasing unsaturated fats increased the eating rate and the relationship was a linear one. Changes in meal frequency or intermeal interval can be attributed to hunger whereas changes in meal size are normally attributed to satiety (Harvatine & Allen, 2006). However, intake of high quality silages resulted in small meal sizes and a short interval between meals to maintain a full rumen.

In contrast, saturated fats increased rumination time by increasing the length of bouts of buccal activity. The mechanism behind this was probably the increased duodenal flow of saturated fatty acid, as suggested by (Harvatine & Allen, 2006).

Diets with high fibre content increased the number of bouts of rumination (14.7 bouts/day vs. 12.1 bouts/day) and bout length (34.8 min/bout vs. 32.1 min/bout) with or without the addition of the rumen inert bulk (these might be plastic bottles or containers used to simulate the fill effect of fibre in the rumen) but it decreased when additional fibre or rumen inert bulk was removed (Dado & Allen, 1995). Low fibre diets increased the number of bouts and the time spent drinking (15.8 bouts/ day;16.6 min/day); high fibre diets, on the other hand, increased time spent eating , chewing and ruminating per unit of DM or NDF intake. In addition, a faster chewing rate (65.0 vs. 62.3chews/min) was observed for high fibre diets (Dado &Allen, 1995)

Dado and Allen (1996) reported feeding behaviour changes in dairy cows fed on low digestible and high digestible fibre diets. The low digestible fibre diets resulted in increased time spent chewing and ruminating (40.3min/bout vs.38.2min/bout) per unit of DMI. There was a reduction in bout number (13.7bouts/day vs. 14.5bouts/day) for diets with low digestible compared with those with a high digestible fibre content. Total time spent chewing, however, was the same for both treatments.

Boudon et al. (2007) described an increased number of meals per day (9.76 vs. 9.16 meals/day) but a decreased amount of DMI per meal (1.59 vs. 1.78 kg) for treatments with or without glucose infusions into the rumen and the duodenum. As meal size was small, inter-meal interval increased (Forbes, 1995; Allen, 2000).

9. Models for predicting voluntary feed intake

A model for predicting feed intake normally consists of a combination of different equations or a single equation representing the complex system of voluntary feed intake in a simplified way (Keady, Mayne & Kilpatrick, 2004). Accuracy in prediction of silage intake and voluntary DMI is crucially important both in practical terms and economically (Yearsly et al., 2001; quoted by Hetta et al., 2007), in order to determine required silage quality (Huhtanen, Rinne & Nousiainen, 2007) and to predict silage DM intake.

Voluntary feed intake models are mainly based on three different components: 1) animal characteristics; 2) feed characteristics; and 3) the feeding environment.

These components have been combined in different ways by different authors. Some authors have described the animal or the feed characteristics (*e. g.* Oldham *et al.,* 1998 (Model 4 Table 4) and Huhtanen, Rinne & Nousiainen, 2007 (Model 7 Table 4)) or both (*e. g.* Vadiveloo and Holmes, 1979 (Model 1 Table 4), Lewis, 1981 (Model 2 Table 4), Dulphy *et al.*, 1989 (Model 5 Table 4) and Mertens, 1987 (Model 6 Table 4)), whilst others have also included the conditions in which feeding took place(*e. g.* Milligan *et al.*, 1981 (Model 3 Table 4)).

Generally these models describe voluntary feed intake as a linear function of animal characteristics such as body weight and production level and a reciprocal function of feed characteristics such as fill effect and energy content (Mertens, 1987). Keady, Mayne and Kilpatrick (2004) compared the results from five different models (Table 4) and evaluated each model's predictive accuracy.

Huhtanen, Rinne & Nousiainen (2007) used the following parameters to predict silage dry matter intake: the D-value (digestible OM in the silage dry matter); the silage fermentation characteristics such as concentration of total acids (VFA and lactic acid *etc.*); and the concentration of DM in the silage. In addition, they also considered the maturity characteristics (first harvest and successive harvests) and the proportion of legume and cereal silages in the grass silage. Silage DM intake was found to be lower in silages from later harvests due to changes in their chemical composition (Huhtanen, Rinne & Nousiainen, 2007). However, in his model, Mertens (1987) treated NDF both from forage and concentrate as the most important parameter for the prediction of DM intake. Total energy requirements of the animal and the energy content of the diet were also a part of the model proposed by Mertens (1987).

Mertens (1987) discussed animal and feed characteristics such as fill capacity of the animal with respect to NDF content of concentrate and forages in the diet; he defined the net energy requirements according to NRC (1978), in which the energy content of diet was determined by chemical analysis. He developed equations for the prediction of intake (Table 4). Energy content of diet and fill effect were inversely related to each other.

The model developed by Milligan *et al.* (1981) was unique because of the inclusion of the temperature of feeding environment and the effect of mud on the body of the animal. When a graph is plotted using theoretical data relating to energy content and fill effect of diet (both dietary characteristics) a negative relationship is apparent.

Table 4. *Comparison of different models, considering various components and the accuracy of the prediction of voluntary feed intake.*

Models	Equations/models	Characteristics included[1]	deviation[2]
1 Vadiveloo & Holmes (1979)	TDMI = 0.076 + 0.404 CDMI + 0.013 LW – 0,129 WL + 4.12 logWL + 0.14 MY	Animal and feed (concentrate only) characteristics	-0.17
2 Lewis (1981)	1) SIP = 0.1035 DM + 0.0516 D – 0.05 N + 45 2) SDMI = 1.068 SIP – 0.00247 C * SIP – 0.00337 (CDMI)^2 -10.9+0.00175 (MY)^2	Animal and feed (both silage and concentrate) characteristics	+ 5.18
3 Milligan *et al.* (1981)	TDMI = (0.0185 SLW + 0.305 MY (0.4 + 0.15PQ)) * (Temp.1) * (MUD 1)	Animal and feeding environment (temperature) characteristics	-12.85
4 Oldham *et al.* (1998)	SDMI = LW* (b1 + (1/ (1 – SDMD) * (b2 + (b3/ SDMD))) – b4 * (C)	Only feed characteristics	-16.98
5 Dulphy *et al.*(1989)	1) CIC = (22 – 8.25exp(-2.02 MY) + (LW – 600) * 0.01) * 0.9 for primiparous and 1.0 for multiparous cows 2) CFV = 1.2 * MY – 0.69 * exp (1.46 FE/FFV) * FFV 3) SDMI = (CIC – CDMI * CFV)/FFV 4) TDMI = SDMI + CDMI	Animal and feed characteristics.	-12.14
6 Mertens (1987)[3]	A = [NDFIC (CNE) – NER (CNDF)] / [NDFIC (CNE – FNE) + NER (FNDF – CNDF)]	Animal and feed characteristics.	.....
7 Huhtanen, Rinne & Nousiainen (2007)[4]	SDMI index = 100 + 10 * [(D-value – 680) * 0.0170 – (TA – 80) * 0.0128 + (0.0198 * (DM – 250) – 0.00002364 * (DM^2 – 250^2)) – 0.44 * a + 4.13 * b – 2.58 * b^2 + 5.90 * c- 6.14 * c^2]	Only feed (silage and different combinations of silages) characteristics	.....

Where model 1: TDMI = total dry matter intake (kg/day), CDMI = concentrate dry matter intake (kg/day), LW = live weight (kg), WL = week of lactation and MY = milk yield (kg/day); model 2: SIP = silage intake potential (g DM/kg), DM = silage dry matter (g/kg), D = silage DOMD (digestible organic matter digestibility) (g/kg), NDF = ammonia NDF (g/kg) and SDMI = silage dry matter intake(kg/day); model 3: SLW = shrunk live weight = live weight * 0.95, PQ = milk fat%, Temp.1 = temperature adjustment and MUD 1 = mud adjustment factor for DMI; model 4: SDMD = silage dry matter digestibility (kg/kg), b1 = 0.01503, b2 = 0.004248, b3 – -0.0004333, b4 = 0.4914 and C = concentrate dry matter intake; model 5: CFV = concentrate fill volume (UE/kg DM), FE = forage energy (UFL/kg DM), FFV = forage fill value (UE/kg DM) and CIC = cow intake capacity (UE); model 6: A = proportion of forage in the diet (expressed as percentage of total diet), NDFIC = NDF intake capacity (kg NDF/d), CNE = concentrate net energy (Mcal * 4.184/kg DM), NER = net energy requirements (Mcal * 4.184/d), CNDF = concentrate NDF (kg NDF/kg DM), FNE = forage net energy (Mcal * 4.184/kg DM), FNDF = forage NDF (kg NDF/kg DM) and CNDF = concentrate NDF (kg NDF/kg DM); model 7: SDMI = silage dry matter index (g/kg DM), TA = total acids (g/kg DM), DM = dry matter (g/kg DM), a = proportion of regrowth silage of silage DM (0-1), b = proportion of legumes in silage DM (0-1) and c = proportion of whole-crop silage of total silage DM (0-1).
[1]Animal, feed and feeding environment characteristics
[2]Deviation between the mean of the observed values and the mean predictions of models, based on information taken from Keady, Mayne & Kilpatrick (2004)

10. Strategies to improve voluntary feed intake

10.1 Maturity stage of forages

The stage of maturity of forage can affect the pattern of utilization of grasses and legume forages. Grasses cut and ensiled at early stage of maturity exhibit rapid fibre and OM degradation in the rumen and higher digestibilities (Rinne, Huhtanen & Jaakkola, 1997; Bernes, Hetta & Martinsson, 2008). In their studies of the effects of grass maturity NDF and OM degradation, Rinne, Jaakkola & Huhtanen, (1997b) showed a curvilinear decrease in OM digestibility from 82.1% for grass forage from earliest cut to 74.7% for the latest cut, examining four maturity stages with cuts at one week intervals. Silage DMI was positively correlated with digestibility, hence the higher intake recorded for grasses cut at the early stages of maturity.

A reduced silage DMI is evident for the regrowth silages (Huhtanen, Rinne & Nousiainen, 2007) since digestibility decreases for each subsequent harvest. An increase of 17.5 g in silage DMI for a 1% increase in silage digestibility has been shown for grasses and legume silages by Huhtanen, Rinne & Nousiainen (2007)s.

In a study conducted by Bernes, Hetta & Martinsson (2008), the *in vitro* degradability of OM (Table 5) was 94.6, 91.3 and 85.8% for early (16 June), mid (20 June) and late (26 June) cuts of Timothy grass, respectively. The study also indicated an increase in DM concentration along with a decrease in metabolizable energy and crude protein content of the grass for every successive cut.

Hetta *et al.* (2007) found a decrease in *in vitro* degradability of OM and NDF as the plant matures. The *in vitro* degradabilities were 88.0 and 86.8% for OM and 81.3 and 78.1% for NDF from the first and second harvests respectively, for dried samples from Timothy grass lays collected during 1999 and 2000.

Table 5. *Effects of maturity of forage on NDF and OM digestibility*

Studies	digestibility %						% decrease in digestibility		description
	First cut		Second cut		Third cut				
	NDF	OM	NDF	OM	NDF	OM	NDF	OM	
Berns, Hetta & Martinsson (2008)	89.4	94.6	85.2	91.3	77.8	85.8	12.9	9.3	1st vs. 3rd cut
Rinne, Huhtanen & Jaakkola (1997a)	75.7	…..	76.5	…..	69.2	…..	8.6	…..	1st vs. 3rd cut
Rinne, Huhtanen & Jaakkola (1997b)	…..	82.1	…..	81.6	…..	75.8	…..	7.7	1st vs. 3rd cut
Jensen *et al.,* (2005)	56.0		51.0		43.0		23.2		1st vs. 3rd cut
Hetta *et al.,* (2007)	81.3	88.0	78.1	86.8	…..	…..	3.9	1.4	1st vs. 2nd harvest
Anne-Maj & Martinsson (2004)	…..	…..	…..	…..	…..	…..	…..	1.28 per day's delay	…..

NDF = Neutral detergent fibre
OM = organic matter

10.2 Type of cereal grains

Different sources of cereal grains exhibit different rumen degradability ranging of the total intake. Grains can be classified as "rapidly and highly rumen degradable" or "slowly and poorly rumen degradable" (Appendix Table II). For example wheat, barley and oats undergo rapid rumen degradation and are digested more completely than maize and sorghum grains (Nocek, 1991; Martin, Philippeau & Michalet-Doreau, 1999). Overall, starch from all cereal sources is degraded by 50-94% in the rumen (Jouany, Michalet-Doreau & Doreau, 2000) depending on the degree and type of processing (*e. g.* 72-94% for rapidly rumen degradable and 50-90% for slowly rumen degradable sources). Martin, Philippeau & Michalet-Doreau (1999) concluded that DMI was reduced by 2.8% for diets fed to beef steers that were supplemented with wheat compared to corn. The ruminal digestibilities were shown to be 86% and 48% for wheat and corn, respectively. In a study conducted by Overton *et al.* (1995), a linear decrease in DM intake from 22.8 kg/day to 19.6 kg/day was observed as maize grains were replaced with barley grains as a supplement to alfalfa silage.

10.2 Processing cereal grains

Processing is always expected to increase rumen and total tract digestibility of cereal grains. Processing can be physical, chemical or a combination of both depending on the nature of the material and the purpose. Maize grains can be fed without processing because the pericarp of maize kernels is not resistant to mastication. However, other cereal grains need to be processed before they are used as supplement to forage based diets or as a part of total mixed ration. It has been shown in a number of studies (Nocek, 1991; Tothi *et al.*, 2003) that processing increases the availability and digestibility of cereal grains.

Physical processing may include grinding, cracking and rolling, which all reduce the particle size of grains and increase potential exposure to bacterial and enzymatic action. Other processing methods may involve grinding or cracking in association with heat and moisture, for example steam-flaking, with the aimof achieving different degrees of starch gelatinisation (Jouany, Michalet-Doreau & Doreau, 2000). However, chemical processing does not always increase rumen digestibility. In fact some chemical treatments (*e. g.* formaldehyde) are used to make grains pass though the rumen so that they are digested and absorbed post ruminally. Processing methods that involve both physical and chemical aspects have proved to be more beneficial by increasing digestibility.

The intensity and nature of grain processing and amount of rumen available starch are the most influential factors controlling voluntary DMI and milk yield (Yang, Beauchemin & Rode, 2001). Processing grains has been shown to affect rumen escape of starch and the post rumen availability. Yang, Beauchemin & Rode (2001) suggested that processing grains, because it alters the availability of rumen degradable starch, could change the pattern of rumen fermentation, resulting in a different acetate to propionate ratio and changes in ruminal pH.

Yang, Beauchemin & Rode (2001) conducted a factorial experiment to study the effects on DMI and total tract digestibilities of flat vs. coarse rolled barley grains.

They recorded an increase of 1.2 kg/day (20.7 vs. 19.5kg) in total DMI, 1.1 kg/day (24.2 vs. 23.1kg) in milk yield and 0.6 kg/day (23.2 vs. 22.6kg) in fat corrected milk yield for flat vs. coarse barley grains. The total tract digestibility of DM, starch and OM were improved by 5%, 10% and 4.4% respectively. The 10% increase in starch digestibility was the result of increased ruminal (33%) and post ruminal (15%) digestion of starch. The more intensive processing to produce flatter barley grains increased both the ruminal and post ruminal digestion of the starch (see Table 6).

Tothi *et al.* (2003) compared the effects of expander processing (Table 6) of barley and maize grains with untreated/unexpanded grains and noted a 4.8% increase in DMI for the treated vs. untreated barley. In fact, expander treatment caused an increase in the post ruminal digestibility of starch grains.

In another study, DM intake in dairy cows was reduced by 3.3% for dry-rolled barley grains compared to whole barley grains, and 5% for temper-rolled compared to whole barley grains (Christen, Hill & Williams, 1996). Although DM intake was reduced, milk yield increased.

Table 6. *Effects of different processing methods on rumen and total tract digestibility of starch, OM and NDF from different starch sources (in situ studies)*

Source	Type of processing	% increase in rumen digestibility			% increase in total tract digestibility			% increase in DMI	% increase in milk yield
		Starch	OM	NDF	Starch	OM	NDF		
Barley[1]	Untreated/rolled	31.6	2.1	-2.6	9.8	8.3	2.2	6.1	4.8
Barley[2]	Untreated/expanded	0.0	.....	.....	0.0	.....	.....	4.8	.....
Barley[3]	Untreated/temper rolled	7.5	23.4	5.6	1.0	6.8	-3.6	-1.5	.....
Barley[4]	Untreated/steam rolled	16.4	8.9	10.4	20.5	14.3	1.8	16.0	20.3
Barley[5]	Temper/dry rolled	.....	.....	.....	4.0	.....	15.0	-3.3	4.8
Barley[5]	Whole/dry rolled	.....	.....	.....	9.0	.....	-6.2	-5.0	6.1
Corn[2]	Untreated/expanded	5.3	.....	.....	14.3	.....	.....	-2.4	.....
Corn[6]	Extruded/ground with two feeds/day	22.0	60.0	24.0	-2.0	6.0	31.0	4.0	4.0
Corn[6]	Extruded/ground with four feeds/day	-8.0	1.0	0.0	-4.0	-8.0	-12.0	10.7	2.3

[1]Rolling (coarse vs. flat) data from (Yang, Beauchemin & Rode, 2001).
[2]Expanding (untreated vs. expanded) data from (Tothi *et al.*, 2003).
[3]Temper rolling (coarse vs. med flat) data from (Beauchemin, Yang & Rode, 2001).
[4]Steam rolling (coarse vs. medium flat) data from (Yang, Beauchemin & Rode, 2000)
[5]Dry vs. temper rolling and tempered whole barley vs. dry rolling data from (Christen, Hill & Williams, 1996)
[6]Extrusion vs. ground processing with two and four feeds per day from (Shabi *et al.*, 1999)
NDF = Neutral detergent fibre
OM = Organic matter
DMI = Dry matter intake

11. Discussion

Restrictions to intake that arise from the physical and chemical characteristics of the feed or from the anatomy or physiology of dairy cows are the main limitations to high DMI and milk production. For diets with low digestibilities (*e. g.* grass and legume forages), voluntary feed intake is regulated by reticulo-rumen capacity, the rate of passage of feed and DM digestibility (Nelson *et al.*, 1968). However, for high digestible diets (*e. g.* cereals and high quality grass and legume silages), voluntary intake seems to be dependent on metabolic weight and production potential. In the form of a simple equation, voluntary feed intake can be expressed as follows:

$$\text{Voluntary feed intake} = \frac{\text{Energy requirements * production potential}}{\text{Energy density of diet * NDF content of diet}}$$

Infusions of different energy sources such as glucose, VFA and starch are usually thought to increase the energy intake of dairy cows. However this is not always the case. For example, in most of the studies the infusion of glucose did not produce any effect on DMI (Forbes, 1995; Allen, 2000), although in other studies, glucose infusions into the rumen or duodenum slightly reduced total DMI (Reynolds *et al.*, 2001; Boudon *et al.*, 2007) but the effects were not significant. The milk yield response was always positive for glucose or starch infusions with an associated reduction in milk fat content.

Mertens, (1987) argued that NDF content could be the single most important dietary parameter for describing reticulo-rumen fill, and proposed that it should be measured in the same units as daily DM intake. It has been concluded that forage based diets increase milk fat content. This can be explained by an altered acetate: propionate ratio in the rumen. On the other hand, cereals are believed to affect the acetate: propionate ratio in favour of propionate. This increased production of propionate is positively correlated with milk yield, but may suppress appetite.

Starch from different cereals can provide readily available energy in the form of glucose. The digestion of starch in the small intestine increases the utilization efficiency of the energy produced (Jouany, Michalet-Doreau & Doreau, 2000). However, the choice of the starch source is very important for maintaining a high level of DM intake and production, since in most of the cases rapidly rumen degradable sources affect the digestion of fibre in the rumen (Nocek and Tamminga, 1991; Overton *et al.*, 1995; Martin, 1999; Jouany, 2000). Since fibre is the main constituent of the forages on which ruminants feed (Van Soest, 1994), intake of fibre directly affects the total DMI.

Processing grains tends to remove the kernels that offer resistance to bacterial attack in the rumen (Beauchemin, Yang & Rode, 2001). In addition, it reduces the particle size and allows them pass easily through the sorting mechanism of the omasum. More DM is consumed if processed grains are used in feed, and in many studies NDF digestibility was also found to be improved. Therefore a surplus of

metabolizable energy was available for the production of more milk. Most of the time, fibre digestibility is negatively related to overall digestibility and the availability of starch in the rumen resulting from grain processing (Christen, Hill & Williams, 1996; Beauchemin, Yang & Rode, 2001; Tothi *et al.*, 2003). In studies where processing decreased fibre digestion, total DM intake tended also to decrease (Table 6). However there is only one study (Shabi *et al.*, 1999) in which DMI was improved and, even then, the total tract digestibility of fibre was decreased.

Altering source of starch, and the degree and type of processing addresses only one aspect of feeding. A high level of intake can also be achieved by adjusting the quality of starch to facillitate a high rate of rumen degradation of grass silage. It has been concluded in many studies (Rinne, Huhtanen & Jaakkola, 1997a; Gustavsson & Martinsson, 2004; Bernes, Hetta & Martinsson, 2008) that the maturity of forages can also influence the rate and extent of the rumen degradation of fibre. It is hypothesised that intake could be increased/maintained at a specific level if the correct sources of starch were combined with forages at an appropriate stage of maturity.

Generally forages are thought to regulate feed intake physically, but the response is totally different in case of grasses cut and ensiled at an early stage of maturity. In a number of studies, grasses cut earlier are associated with a faster rate of degradation and passage of both NDF and OM (Rinne, Huhtanen & Jaakkola, 1997b; Hetta *et al.,* 2007). Bernes, Hetta & Martinsson (2008) concluded that Timothy grass cut before heading stage increased silage DMI and live weight gain in lambs. Many other studies confirm the increased DMI associated with early cut grass and cereal silages in dairy cows (Jensen *et al.*, 2005; Kuoppala *et al.*, 2008). Maturity of plants causes to increase the proportion of plant carbohydrates, and causes to change the chemical composition of cell walls (Rinne, Huhtanen & Jaakkola, 1997). As a result of these changes DM and NDF concentration in the whole plant is increased in silages made from mature forages. Hetta *et al.,* (2007) found a negative correlation between DM concentration and *in vitro* OM degradability (0.17), and between NDF concentration and *in vitro* OM degradability (0.169, for dry samples of mature Timothy grass.

It has also been reported that silage fermentation characteristics during ensiling vary with increasing maturity of grasses. The degradation of the NDF fraction has been found to be more pronounced for early cut grass than for mature grasses. The concentration of total fermentation acids decreased from 102 g/kg DM to 59 g/kg DM for grass harvested four weeks later (Rinne, Jaakkola & Huhtanen, 1997). The work of Kuoppala *et al.* (2008) also demonstrated a decrease in the concentration of total acids from 88 g/kg DM to 50 g/kg DM for primary growth silage cut at early and late stage. Mature cut silages may also be characterised by a decrease in the nitrogen content of plants with increasing maturity, indeed a negative correlation between the two (0.23) was stated by Hetta *et al.* (2007). But, on the same time, increased nitrogen losses has been recorded for early cut silages during rumen degradation in dairy cows (Rinne, Jaakkola & Huhtanen, 1997).

The characteristics of silage that are important for silage DMI can be ranked on the basis of information provided by Huhtanen, Rinne & Nousiainen (2007). The D-value or digestibility of silage may be the most important feature of all, followed by the quality of NDF, silage fermentation quality, DM concentration and proportion of legume or whole-crop cereals. The first two factors may be related directly or indirectly to the maturity stage of the grasses. Further investigations are needed to determine the quality of starch in relation to the maturity stage of forages.

Most of the models reviewed in this study included animal, feed and feeding environment characteristics (Table 4), and an output variable such as milk yield as the basis for predicting feed intake (the input variable). But none of these models includes examines the interactions between nutrients from different origins. However the model developed by (Huhtanen, Rinne & Nousiainen, 2007) provides a good picture of silage DMI, taking into account the silage quality and proportion of different silages substituted for grass silage. It is therefore recommended that information about different cereal concentrate sources and their effects on fibre digestion, and on total DMI should also be included in future models for predicting of voluntary feed intake in lactating dairy cows.

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Acknowledgements

Appendix

Table I. Various methods for the determination of non-structural carbohydrates in different feed stuffs (grains, by-products, and forage sources) (% of DM)

Different feed stuffs	Total carbohydrates[1]			Non-structural carbohydrates[2]			Starch[3]		
	Number of studies	mean	Standard deviation	Number of studies	mean	Standard deviation	Number of studies	mean	Standard deviation
Grains and by-products									
Alfalfa dehydrated	.....	.....	.....	1	22.5	....	......	.....	.....
Barley	3	69.4	5.7	4	58.0	2.8	15	60.6	10.5
Beans, horse	.....	.....	.....	1	63.0	.....	5	39.2	3.5
Beet pulp	3	10.7	0.2	2	29.1	1.8	1	1.5	.....
Brewers dried grains	4	15.7	1.7	2	13.5	0.1	1	3.8	.....
Corn									
Corn cobs	1	15.5	.....	2	10.3	6.9	.....		
Grain, ground	6	74.6	1.7	3	73.7	2.1	24	76.1	8.8
HM[4]	.....			1	75.1	.....	6	79.0	9.1
HM ground ear	.....			2	58.4	1.4	.....		
Hominy	3	59.5	7.8	2	52.0	5.6	1	31.0	.....
Soluble	1	13.9	.....	1	30.3	.....	.....		
Gluten feed	5	21.6	4.3	2	23.3	5.3	1	40.3	.....
Gluten meal	4	19.4	2.2	2	14.5	0.2	1	20.5	.....
Distillers' grains corn	4	10.5	1.7	2	14.1	2.5	.....		
Linseed meal	.....			2	26.8	2.7	2	2.8	8.5
Millet	.....			1	63.3	.....	2	63.7	2.9
Oats	3	56.9	0.1	2	46.5	0.8	7	42.1	3.7
Peanut meal	3	59.7	4.2	2	25.2	1.6	2	4.4	1.1
Rice									
Bran	.....			1	25.0	.....	1	26.9	.....
Grain	.....			1	73.8	.....	1	84.8	.....
Sunflower meal	.....			2	26.6	.....	2	13.0	6.0
Sorghum grain	.....			2	69.9	5.5	4	75.4	8.7
Wheat									
Bran	3	28.0	9.2	2	20.8	0.3	2	13.3	0.2
Flour	.....			.....			1	77.2	.....
Grain	.....			2	69.0	2.8	6	64.1	3.7
Middling	3	48.3	0.2	2	35.0	0.9	1	23.8	.....
Forages									
Alfalfa									
Hay	3	8.7	0.2	6	24.3	1.1	1	2.2	.....
Silage	5	5.8	3.8	2	24.7	0.8	2	8.1	7.2
Corn silage	3	32.0	3.8	6	36.1	7.0	5	39.4	9.5
Oat silage	.....			1	14.9	.....	2	9.5	6.8
Timothy hay	1	1.4	.....	5	10.1	2.8	2	2.9	1.9
Wheat straw	.....			1	1.8	.....	.....		

[1]Literature value determined by enzymatic methods
[2]Determined by difference equations: 100- (NDF + protein + lipids + ash), analytical values from NRC (89)
[3]Literature value determined by various enzymatic methods using bacterial amylase
[4]High moisture
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Table II. Rumen degradable starch (% of total starch) values for various feedstuffs determined by *in vitro, in situ, or in vivo* methods.

Feed stuffs	In situ and in vitro			In vivo		
	Number of studies	means	Standard deviation	Number of studies	means	Standard deviation
Barley						
Ground	3	89.9	6.2	4	87.9	4.6
Rolled	.....			8	87.2	2.5
Beans, faba	3	74.2	4.4	.....		
Canola meal	1	72.5	.....	.....		
Corn						
Whole	.....			5	62.6	9.9
Cracked	.....			2	65.0	5.6
Ensiled, shelled	1	72.0	......	3	86.0	3.0
Ground	5	58.4	5.1	11	76.4	12.1
Rolled, wet	.....			1	68.3	.....
Rolled	1	51.0	.....	5	76.8	5.0
Steam-flaked	1	87.0	.....	5	85.6	5.0
Hominy	2	66.2	6.4	.....		
Silage	1	69.6	.....	4	82.0	9.5
Corn gluten feed	3	80.6	0.8	.....		
Corn gluten meal	1	86.5	.....	.....		
Oats	2	94.3	6.6	2	84.0	11.1
Peas	2	75.8	2.1	.....		
Sorghum						
Grain, ground	2	54.2	4.4	9	67.3	17.5
Ensiled	.....			1	86.2	.....
Rolled	.....			9	64.0	9.6
Steam-flaked	.....			7	82.6	8.3
Rice						
Bran	3	71.3	3.3	.....		
Grain	1	68.0	.....	.....		
Rye	.....			1	90.2	.....
Wheat						
Bran	1	88.2	.....	.....		
Grain	3	90.5	7.3	5	89.3	2.1
Flour	2	88.3	0.6	.....		
Middlings	2	88.8	0.8	.....		

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