Rumen Development in the Dairy Calf

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Take Home Messages

- Young calves have undeveloped rumens at birth and must undergo physiological changes before they can digest high fiber feeds.
- Concentrate feeds are digested to propionic and butyric acids in the rumen and stimulate the growth of the rumen papillae.
- Digestion of milk and forages does not provide the end products needed to develop the rumen papillae.
- After concentrate feeding begins, 3 to 4 weeks of rumen development is needed before the calf is able to digest substantial amounts of dry feeds.

Introduction

The degradation of feedstuffs, rumen microbial synthesis, and the various resulting end products have been a subject of investigation for over a century. In 1884, Tappiener (as cited in Phillipson, 1947) attributed cellulose digestion in the rumen to digestive actions of symbiotic organisms in the rumen. Much work followed these early discoveries, devoted primarily to describing the digestion of cellulose, the assimilation of various end products of the microbial population, and the various species of rumen bacteria that exist under certain rumen conditions.

Young calves are unique in that at birth they are physically and functionally two different types of animals with respect to their gastro-intestinal system. At birth the physical attributes distinguishing a ruminant from a monogastric animal, i.e. the reticulum, rumen, and omasum, are present. However, the rudimentary state of the reticulo-rumen and omasum, presence of the esophageal groove (Church, 1988), plus the developing abomasal and intestinal enzymatic state forces neonatal ruminants to function as monogastric animals (Longenbach and Heinrichs, 1998) subsisting on milk-based diets, which are digested and assimilated quite efficiently (Davis and Drackley, 1998). Digestive enzymatic changes coupled with the high daily costs of maintaining a preweaned calf (Gabler et al., 2000) result in an ability and need to transition the calf from a monogastric animal to a ruminant. A smooth transition from a monogastric to ruminant animal, with minimal loss in growth, requires adequate size and development of the reticulo-rumen for efficient utilization of dry and forage-based diets. Therefore, understanding the factors responsible for initiating cellular growth and maturation of the non-functional rumen tissues and establishing rumen development and function in the neonatal calf are important.

▪ Rudimentary Reticulo-Rumen

At birth, the reticulum, rumen, and omasum are undeveloped, nonfunctional, small in size compared to the abomasum, and disproportionate to the adult digestive system. Papillary growth, rumen muscularization, and rumen vascularization are minimal to nonexistent, the rumen wall is thin and slightly transparent, and reticulo-rumen volume is minimal (Warner et al., 1956). Ruminant animals require a physically and functionally developed rumen to meet the demands of an innate desire to consume forages and dry feeds. However, the neonatal rumen will remain undeveloped if diet requirements for rumen development are not provided. Rumen development appears to be greatly affected by diet and dietary changes (Harrison et al., 1960). In addition, the influence of dietary factors on rumen development may vary, and development of rumen epithelium, rumen muscularization, and expansion of rumen volume have been found to occur independently (Stobo et al., 1966). These findings suggest that dietary factors influencing papillary growth and development may not affect rumen muscularization or rumen volume.

▪ Changes in Rumen Epithelium

Proliferation and growth of squamous epithelial cells causes increases in papillae length, papillae width, and thickness of the interior rumen wall (Church, 1988). Figure 1 demonstrates the progression of cellular differentiation and growth that occurs during the first few weeks of life in samples taken from the cranial dorsal sac of young calves.

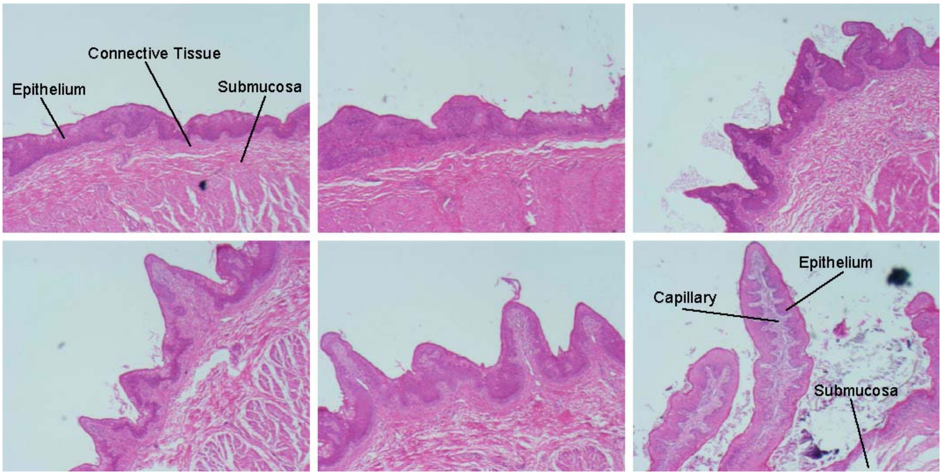

Figure 1. The progression of cellular differentiation and growth during the first weeks of life in a grain fed dairy calf. (progression is 3d to 35d of age, upper row L to R, lower row L to R.

Prior to transitioning from a pre-ruminant to a ruminant, growth and development of the ruminal absorptive surface area (papillae), is necessary to enable absorption and utilization of microbial digestion end products, specifically rumen volatile fatty acids (Warner et al., 1956). Presence and absorption of volatile fatty acids is indicated to stimulate rumen epithelial metabolism and may be key in initiating rumen epithelial development (Baldwin and McLeod, 2000). However, it has been suggested that rumen epithelial ketogenesis, indicating metabolic activity, may occur independently of volatile fatty acid production. Nevertheless, numerous researchers have indicated that ingestion of dry feeds and the resultant microbial end products sufficiently stimulate rumen epithelial development (Greenwood et al., 1997; Nocek et al., 1984). However, the stimulatory effects of different volatile fatty acids are not equal, with butyrate being most stimulatory, followed by propionate. Butyrate metabolism by the epithelium appears to increase concomitantly with decreasing rumen pH and increasing butyrate concentrations (Baldwin and McLeod, 2000). A continuous presence of volatile fatty acids maintains rumen papillae growth, size, and function (Warner et al., 1956). Therefore, it is likely that diets composed of milk, concentrates, or forages affect the rate and extent of rumen epithelial growth differently.

Papillae length and width are the most obvious factors influencing absorptive surface area, but changes in papillae density also should be considered. Dietary and age differences have been found to alter papillae density of the developing rumen; however, significant differences due to dietary treatment are seldom reported for papillae density in calves (Lesmeister et al., 2004a). Papillae density is commonly reported as the number of papillae in a fixed area (usually 1 cm^2), regardless of rumen volume, and rumen volume has been shown to increase with age. Lesmeister et al. (2004a) demonstrated a procedure for sampling rumen tissue that was capable of detecting treatment differences for papillae length and width and moderately capable of detecting treatment differences for rumen wall thickness. Minimal treatment influence on papillae density may be explained by a confounding effect of rumen volume. In addition, McGavin and Morrill (1976) and Lesmeister et al. (2004a) reported intra-rumen variation for papillae measurements, demonstrating that papillae growth is not universal in all rumen areas.

▪ Liquids Feeds and Rumen Development

Milk or milk replacer is initially the primary diet of neonatal dairy calves; however, its chemical composition and the shunting effect of the esophageal groove limit its ability to stimulate rumen development (Warner et al., 1956). Numerous researchers have reported minimal rumen development in calves receiving solely milk or milk replacer even up to 12 weeks of age (Tamate et al., 1962), and others have reported a regression, or stasis, of rumen development when calves were switched from a dry to milk/milk replacer diet (Harrison et al., 1960). In addition, calves receiving only milk/milk replacer exhibit minimal rumen epithelial metabolic activity and volatile fatty acid absorption, which once again does not increase with age. However, ruminal size of the milk-fed calf, regardless of rumen development, has been shown to increase proportionately with body size (Vazquez-Anon et al., 1993). Therefore, while a milk/milk replacer diet can result in rapid and efficient growth, it does little to prepare the pre-ruminant calf for weaning or utilization of grain and forage based diets.

▪ Solid Feeds and Rumen Development

Solid feeds, unlike liquid feeds, are preferentially directed to the reticulo-rumen for digestion (Church, 1988). Solid feed intake stimulates rumen microbial proliferation and production of microbial end products, volatile fatty acids, which have been shown to initiate rumen epithelial development. However, solid feeds differ in their efficacy to stimulate rumen development. Chemical composition of feeds and the resultant microbial digestion end products have the greatest influence on epithelial development (Nocek et al., 1984).

Multiple chemical characteristics of solid feeds appear to influence rumen epithelial growth. Concentrates and diets containing casein, starch, cellulose, and minerals have increased the rate of rumen development when compared to forage sources. When introduced into the rumen as purified sodium salts, sodium butyrate had the greatest influence on rumen epithelial development, followed by sodium propionate; sodium acetate and glucose had minimal effects. In addition, research has identified butyrate and propionate as the volatile fatty acids most readily absorbed by rumen epithelium, especially when present at physiological concentrations (Baldwin and McLeod, 2000). Furthermore, the chemical composition of concentrates causes a shift in the microbial population, subsequently increasing butyrate and propionate production at the expense of acetate. Increased microbial production of stronger acids, i.e. lactate, butyrate, and propionate, also decreases rumen pH.

Forages, on the other hand, have an increased ability to maintain a higher ruminal pH, due to a larger particle size and increased fiber content (Zitnan et al., 1998). Maintenance of a higher ruminal pH supports microbial populations typically associated with forages, which in turn shifts volatile fatty acid production from butyrate and propionate to acetate. There are many studies indicating increased rumen epithelial development when fatty acid salts of butyrate and propionate are fed.

Increased absorption and utilization of butyrate and propionate over acetate provides further evidence that the former volatile fatty acids stimulate epithelial development (Baldwin and McLeod, 2000). Whether the actual stimulant for epithelial development is increased butyrate and propionate production, a decreased ruminal pH concomitant with stronger ruminal acid production, or a combination; concentrates appear to result in greater rumen epithelial development than forages. This concept is demonstrated in Figure 2, which shows the marked differences in rumen development of 6 week old calves fed milk, milk and grain, or milk and forage (dry hay).

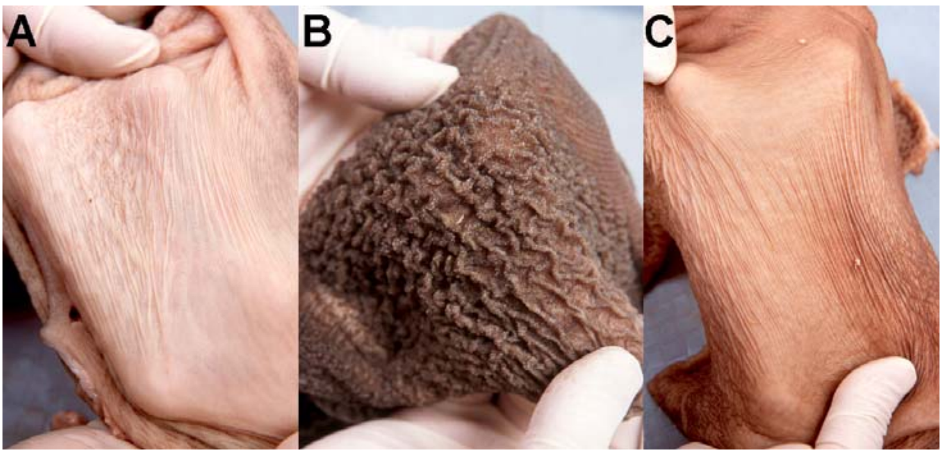

Figure 2. Comparison of rumen papillae development at 6 weeks in calves fed milk only (A), milk and grain (B), or milk and dry hay (C).

Recent studies have looked at dietary alterations or additions and their effect on rumen development and its subsequent effects on rumen microbial end products. While addition of yeast culture increased calf grain intake, it did not appear to significantly affect rumen development in young calves when added at 2% of the diet (Lesmeister et al., 2004b). Papillae length and rumen wall thickness were significantly greater in 4 week old calves fed calf starters containing steam-flaked corn over those fed dry-rolled and whole corn when these corn supplements made up 33% of the calf starter (Lesmeister and Heinrichs, 2004). This study showed that the type of grain processing can influence rumen development in young calves.

Physical Structure and Rumen Development

Rumen epithelial development cannot be thoroughly discussed without covering the influence of parakeratosis on papillae development and absorptive ability. Parakeratosis occurs when epithelial squamous cells develop a hardened keratin layer due to a diet's inability to continuously remove degenerating epithelial cells (Hinders and Owen, 1965). Parakeratosis creates a physical barrier, restricting absorptive surface area and volatile fatty acid absorption, reducing epithelial blood flow and rumen motility, and causing papillae degeneration and sloughing in extreme cases (Beharka et al., 1998). Initial evidence of parakeratosis is papillae clumping and branching, followed by papillae degeneration and sloughing (Anderson et al., 1982; Zitnan et al., 1998). Concentrate diets with small particle size and low abrasive value (Greenwood et al., 1997) increased volatile fatty acid production, decreased rumen buffering capacity, and subsequently decreased rumen pH (Anderson et al., 1982) are factors commonly associated with occurrences of parakeratosis. Abrasive value has been defined as a feed's efficacy in physically removing keratin and/or dead epithelial cells from the rumen epithelium (Greenwood et al., 1997). Therefore, increased feed particle size, especially with forages or coarsely-ground concentrates, maintains epithelial and papillae integrity and absorptive ability via physical removal of the keratin layer, increased rumination and rumen motility, increased salivary flow and buffering capacity, and development of mature rumen function and environment. However, factors such as individual animal susceptibility, intake differences, passage rate, rumination rate, and salivary production may also contribute to occurrences of parakeratosis (Zitnan et al., 1998).

Changes in Rumen Muscularization and Volume

Feed physical structure likely has the greatest influence on development of rumen muscularization and volume. Stimulation of rumen motility is governed by the same factors, particle size and effective fiber, in the neonatal ruminant as in the adult ruminant (Beauchemin and Rode, 1997). In contrast to concentrate's advantages for epithelial development, forages appear to be the primary stimulators of rumen muscularization development and increased rumen volume (Zitnan et al., 1998). Large particle size, high effective fiber content, and increased bulk of forages or high fiber sources physically increase rumen wall stimulation, subsequently increasing rumen motility, muscularization, and volume (Vazquez-Anon et al., 1993; Warner et al., 1956; Zitnan et al., 1998). As discussed earlier, increases in rumen muscularization and volume have occurred independently of epithelial development. Supporting evidence for independent muscle and epithelial growth is found in studies determining the effects of inert material (sponges, toothbrush bristles, or bedding) on rumen epithelial, muscular, and capacity development. Inert materials were found ineffective for stimulating papillae growth, but capable of significantly increasing rumen capacity and muscularization (Harrison et al., 1960). However, solid feeds other than forages or bulky feedstuffs can be effective in influencing rumen capacity and muscularization. Coarsely or moderately ground concentrate diets have been shown to increase rumen capacity and muscularization more than finely ground or pelleted concentrate diets, indicating that extent of processing and/or concentrate particle size affects the ability of concentrates to stimulate rumen capacity and muscularization (Beharka et al., 1998; Greenwood et al., 1997). Therefore, concentrate diets with increased particle size may be the most desirable feedstuff for overall rumen development, due to their ability to stimulate epithelial development, rumen capacity, and rumen muscularization.

While the basics of rumen development have been published in the literature, current rumen development research focuses on dietary manipulation, attempting to optimize the rate and extent of rumen development. Increased availability of feed by-products, development of new feed additives, and differences in calf starter particle size all provide areas for future rumen development research. Understanding the cellular biology and physiological changes that occur during rumen development, clarifying neonatal calf digestion kinetics, and development of low-impact or non-invasive research procedures could be instrumental in advancing this area further. While much is known related to rumen development, several areas require additional study. The adoption of newer technologies to stimulate the rate of rumen development may have important economic consequences for dairy and beef producers and warrant further applied research studies.

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