

# **Understanding Dietary Fiber: The role of forage fiber in rumen development and heifer growth.**

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Raising dairy heifers from birth to calving has been found to comprise the second largest expense on the dairy farm towards the production of milk (Heinrichs, 1993) and therefore require a reasonably high level of attention on a commercial dairy farm. The focus of this paper will be feedstuffs, in particular limiting forages for the development of the rumen in the neonate, as well as a possible system for older heifer growth where high quality forages are included in the diet on a very limited basis.

*The Neonate Dairy Calf*

Neonatal ruminants 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. 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; Van Soest, 1994). Digestive enzymatic changes coupled with the high daily costs of maintaining a preweaned calf result in an ability and need to transition the calf from a monogastric animal to a ruminant animal (Church, 1988). A smooth transition from a monogastric to ruminant animal, with minimal loss in growth, requires adequate development of the reticulo-rumen for efficient utilization of dry and forage-based diets.

At birth, the reticulum, rumen, and omasum are undeveloped, nonfunctional, small in size when compared to the abomasum, and disproportionate to the adult digestive system (Tamate et al., 1962). Rumen development appears to be greatly affected by diet and dietary changes (Brownlee, 1956). 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 (Flatt et al., 1958). These findings suggest that dietary factors influencing papillary growth and development may not affect rumen muscularization or rumen volume.

Proliferation and growth of squamous epithelial cells causes increases in papillae length, papillae width, and thickness of the interior rumen wall (Church, 1988). 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 (Church, 1988). 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). Numerous researchers have indicated that ingestion of dry feeds and the resultant microbial end products sufficiently stimulates rumen epithelial development (Nocek et al., 1984; Warner et al., 1956). However, the stimulatory effects of different volatile fatty acids are not equal, with butyrate being most stimulatory, followed by propionate. Low activity of the acetyl-CoA synthetase enzyme appears to limit rumen

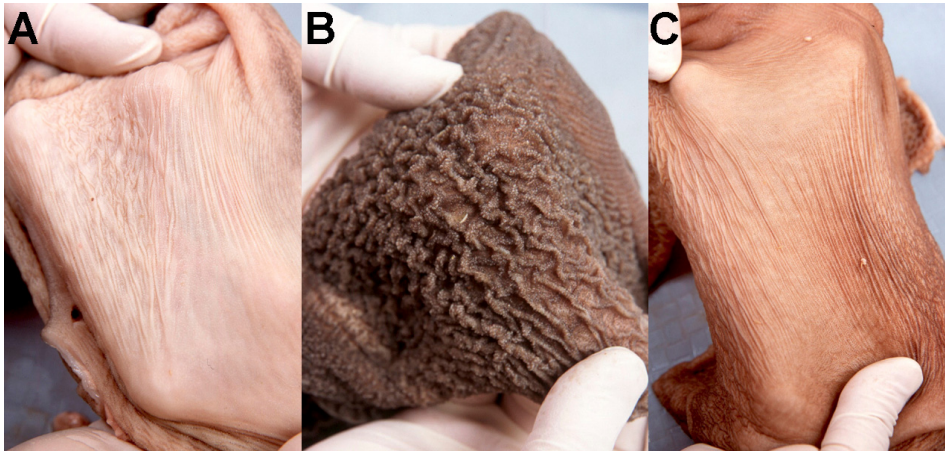
epithelial metabolism of acetate; thereby limiting acetate's ability to stimulate epithelial development (Harmon et al., 1991). Conversely, Baldwin and McLeod (2000) indicated comparable acetate and butyrate metabolism in sheep, stating that animal energy status may influence individual volatile fatty acid metabolism rate. However, the millimolar concentration of acetate was higher than butyrate in this study, indicating a possible conditioning of the rumen epithelium to acetate use, due to decreased butyrate availability. In addition, epithelial butyrate metabolism 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, and such results have been reported (Harrison et al., 1960).

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 (Tamate et al., 1962; 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, unlike liquid feeds, are preferentially directed to the reticulo-rumen for digestion (Church, 1988; Van Soest, 1994). 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 (Pounden and Hibbs, 1948). However, solid feeds differ in their efficacy to stimulate rumen development. Chemical composition of the feeds, and the resultant microbial digestion end products, has the greatest influence on epithelial development (Harrison et al., 1960; Warner et al., 1956). A lower rumen pH and its effect on volatile fatty acid absorption may be the catalyst driving rumen epithelial growth (Sutton et al., 1963). However, dietary type, microbial population present, and volatile fatty acids produced (Hibbs et al., 1956) greatly influence ruminal pH and cannot be removed from the equation.

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; Sander et al., 1959). Whether the actual stimulant for epithelial development is increased butyrate and propionate production (Tamate et al., 1962), a decreased ruminal pH concomitant with stronger ruminal acid production, or a combination; concentrates appear to result in greater rumen epithelial development than forages (Warner et al., 1956; Zitnan et al., 1998). This concept is demonstrated in Figure 1, which shows the marked differences in rumen development of 6 week old calves fed milk, milk and grain, or milk and forage (dry hay).

Recent studies have looked at dietary alterations or additions and their effect on rumen development and its subsequent effects on rumen microbial end products. 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)



**Figure 1.** Comparison of rumen papillae development at 6 weeks in calves fed milk only (A), milk and grain (B), or milk and dry hay (C).

This study showed that the type of grain processing can influence rumen development in young calves but have few other distinct differences in the overall growth and intake of the calf.

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 (Van Soest, 1994). In contrast to concentrate's advantages for epithelial development (Nocek et al., 1984; Warner et al., 1956), 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). 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 (Harrison et al., 1960). Inert materials were found ineffective for stimulating papillae growth, but capable of significantly increasing rumen capacity and muscularization. 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. 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.

### *The Growing Heifer*

Since feed costs make the greatest contribution to the expenses associated with raising heifers; comprising about 60% of the all heifer expenditures (Gabler et al., 2000), it would follow that a reduction in feed costs could significantly contribute to decreasing the overall monetary expenditure for raising dairy heifers. Therefore, many of the experiments involving dairy heifers have focused on ways to minimize the costs associated with the growth period or hastening the onset of the productive period.

There is currently very little data in the literature concerning the effects of feeding high forage (HF) or high concentrate (HC) rations, when delivered for the same level of growth, on responses obtained from dairy heifers. Reynolds et al. (1991c; 1991e) investigated the effects of differing the proportions of forage and concentrate in rations fed to growing beef heifers on energy metabolism at the level of the whole animal as well as for the portal drained viscera tissues and the liver. Reynolds et al. (1991d) found that when fed a constant level of metabolizable energy, heat production was lower for the animals fed the HC ration (25:75 vs. 75:25 forage:concentrate) resulting in a significantly increased tissue energy accretion. The portal-drained viscera (PDV) accounted for proportionately less oxygen consumption for the HC ration, however the total splanchnic tissue (TST) consumption of oxygen did not differ between diets. Glucose release to the periphery was also significantly increased when feeding a HC ration, possibly due to the decreased glucose metabolism by the PDV as glucose output by the liver was not significantly different between diets (Reynolds et al., 1991b). While nitrogen dynamics were discussed, the responses are difficult to resolve or to ascribe to a particular forage-to-concentrate ratio due to differences in nitrogen intake between treatments. Of note however, is that, while nitrogen intake was greater for the HF ration, tissue retention of nitrogen was the greatest for the HC ration. Relative to intake, heifers fed the HF ration excreted more fecal dry matter, nitrogen, and energy and more urinary nitrogen. While it is unclear if the improved nitrogen efficiencies are due to differences in nitrogen intake, the flow of some nitrogen containing compounds (ammonia,  $\alpha$ -amino nitrogen, and urea) across the PDV were not significantly affected by the treatment rations fed, indicating that post-absorptive nitrogen efficiency may be improved by low forage rations.

Reynolds et al. (1991a) also found that the maximal contribution of amino acid to gluconeogenesis tended ( $P < 0.10$ ) to be reduced and significantly less ( $P < 0.05$ )  $\alpha$ -amino acid N was removed by the liver in the heifers fed the HC ration. Similarly, Huntington et al. (1996) fed iso-nitrogenous and iso-energetic diets to six multi-catheterized beef steers to investigate the dynamics of nitrogen when fed varying proportions of forage and concentrate. In a comparison of diets containing 63 or 37% forage, significantly more urea nitrogen and glucose was released by the TST to the periphery when fed 37% forage, while acetate release was significantly reduced. Amino acid release by the TST was greater for the low forage diet, however statistical significance was not attained.

A typical dairy heifer is fed a ration in which the majority of its nutrition is derived from forages as opposed to concentrated feedstuffs. However, there is a large inefficiency associated with this method of feeding due to lower digestibility of most forages, greater metabolic protein and energy requirements associated with digesting

forage, and higher feed costs per unit of energy as compared to concentrates. The potential therefore exists to replace a significant proportion of the forage DM in a ration with concentrate DM, reducing the inefficiency associated with raising dairy heifers while maintaining similar ADG. To address this concept for raising dairy heifers, a series of experiments have recently been conducted to evaluate heifer growth characteristics and nutrient utilization when given HF or HC rations at restricted intakes to achieve a similar ADG.

To test the effects of restricting the intake of feed to dairy heifers, irrespective of the level of dietary forage and concentrate, we recently conducted an experiment, the objective of which was to determine the effects of differing intakes of dry matter on the nutritional and nitrogen efficiency in growing dairy heifers (Zanton and Heinrichs, 2004; Zanton and Heinrichs, 2005). Organic matter digestibility was linearly increased ( $P < 0.05$ ) by decreasing levels of DMI, while NDF digestibility was unaltered by treatment. Nitrogen excretion in the feces and urine increased linearly ( $P < 0.05$ ) with increasing intake of nitrogen and dry matter. Nitrogen retained as either a proportion of nitrogen consumed or nitrogen apparently absorbed was quadratically affected by treatment ( $P < 0.05$ ) with nitrogen efficiency peaking at intermediate levels of intake.

To further address the concept of restricting intake for dairy heifers on productive efficiency, experiments have recently been conducted to evaluate heifer growth characteristics and nutrient utilization when given rations of high or low energy density for similar levels of ADG. The objective of the first experiment (Zanton and Heinrichs, 2006a) was to elucidate the effects feeding different a HC or a HF ration at restricted intakes on feed efficiency and growth characteristics, and the effects on first lactation milk yield. Less DM was consumed by the heifers fed HC than for HF (5.41 HC vs. 5.95 HF kg/d  $\pm$  0.11;  $P < 0.01$ ) at similar ADG leading to significantly improved feed efficiency for the heifers receiving HC ( $P < 0.01$ ). Daily gains of skeletal measurements were not different between treatments. From these results we conclude that feeding a HC ration leads to similar growth performance when the level of intake is restricted to achieve a controlled ADG. Reproduction and first lactation data are currently being monitored.

Given the nutritional efficiency that we observed to arise by feeding HC rations at restricted intakes, we conducted a study to evaluate the effects feeding different forage and concentrate levels on feed and nitrogen efficiency and on nitrogen utilization and ammonia volatilization from the resulting manure. We hypothesized that energy and nitrogen provided in a HC ration would be utilized with a greater efficiency than when an equivalent amount of energy and nitrogen is given in a high forage ration. Greater utilization of nitrogen by the animal, we further hypothesized, would lead to reduced nitrogen excretion and therefore reduced ammonia emissions into the environment. The experiment (Zanton and Heinrichs, 2006b; 2006c) was designed as a split plot design with Young (Y; 313  $\pm$  4d; 263  $\pm$  6kg) and Old (O; 666  $\pm$  8d; 583  $\pm$  6kg) heifer blocks given HC and HF twice daily to four cannulated heifers per block for four, 28d periods. Both the HC and the HF rations contained the same feed ingredients, but in differing proportions, yielding two treatment rations containing 75 or 25 percent of the ration dry matter as forages. The treatment rations were restricted to provide 0.22 Mcal ME and 1.9 g N per kg EBW<sup>0.75</sup>.

Organic matter intake was lower for heifers fed HC ( $P < 0.01$ ), however due to improved OM digestibility (75.97 HC vs. 71.53 HF  $\pm$  0.70%;  $P < 0.01$ ), intake of digestible OM was not different between treatments ( $P > 0.20$ ). NDF digestibility was not

significantly affected by dietary treatment (52.92 HC vs. 51.18 HF  $\pm$  1.46%;  $P>0.20$ ). The heifers fed HF had increased total rumen content wet weight (37.84 HC vs. 42.18 HF  $\pm$  1.36kg;  $P<0.01$ ). Total VFA concentrations were not altered by dietary treatment (110.80 HC vs. 112.87 HF  $\pm$  5.00 mM;  $P>0.14$ ). Similar concentrations of total VFA occurred due to higher acetate concentrations, lower butyrate concentrations (both  $P<0.01$ ), and a tendency for reduced propionate concentrations ( $P>0.07$ ) in HF. Mean rumen pH was lower for HC (6.24 HC vs. 6.51 HF  $\pm$  0.10;  $P<0.01$ ) and the amount of time that the pH was lower than 6.00 was greater in HC (7.12 HC vs. 3.15 HF  $\pm$  1.84 hr.;  $P<0.01$ ).

Fecal N excretion tended to be greater for HF ( $P<0.06$ ) and urinary N excretion was not affected by treatment ration ( $P>0.20$ ), leading to greater overall N retention for heifers fed HC ( $P<0.01$ ). The efficiency of N retention (0.2740 HC vs. 0.2126 HF  $\pm$  0.0128 g N retained/g N consumed;  $P<0.01$ ) and the environmental N load (2.92 HC vs. 4.72 HF  $\pm$  0.43 g N excreted/g N retained;  $P<0.01$ ) were also significantly improved in heifers receiving HC. The ammonia volatilization rate, when adjusted to reflect the greater production of urine and feces by HF, was greater for heifers fed HF (28.74 HC vs. 33.15 HF  $\pm$  1.00g/d;  $P<0.01$ ). We conclude that feeding HC can produce changes in rumen fermentation in Y and O heifers, but the magnitude of these changes can be reduced by restricting intake. We further conclude that Y and O heifers fed HC will have improved efficiency of OM and N utilization when intake is controlled. Other experiments using corn silage as the sole source of forage have shown similar results (Daubert et al., 2006; Moody et al., 2006). Overall, utilizing HC compared to HF rations, fed to maintain optimum levels of daily gain, have shown that whole body growth and skeletal measurements were unaffected, feed costs dropped between 3 and 16%, and manure output fell between 12 and 40% (depending on feedstuffs used). No detrimental effects, either short or long term, were noted from this feeding management system.

Our studies have shown that feeding high concentrate, low forage rations in a restricted manner to growing dairy heifers from 4 to 22 months of age leads to similar growth performance with respect to weight gains and structural growth. In addition, recent studies by Hoffman et al., (2007) has shown that restricted high concentrate rations (40% concentrate) can also improve feed efficiency and reduce manure production without negative effects on lactation. These results also lead to the overall conclusion that provided the level of intake is restricted to allow for an optimal level of ADG, higher concentrate rations can be fed to dairy heifers resulting in reduced feed costs and reduced levels of nutrient waste.

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