Adaptive Changes of the Ruminal Mucosa and Their Functional and Clinical Significance

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It has been known for some time that the ruminal mucosa undergoes proliferative or reductive processes depending on the type of feed (3, 8, 10, 12, 16, 22). The volatile fatty acids, in particular propionic and butyric acid, produced during the bacterial decomposition of the ingested carbohydrates, are responsible for the development of the ruminal mucosa in calves and for the structure of the mucosa of older animals (8, 13, 17, 18, 19). Of particular interest from the clinical point of view are the excessive proliferation processes in the form of ruminal parakeratosis and chronic hyperplastic ruminitis (4, 22).

Various observations indicate that the changes seen in the tissue of the mucosa are of functional significance and primarily influence the absorption of volatile fatty acids produced in the reticulo-rumen (1, 21, 23). In intensively fed calves with parakeratotic ruminal mucosa, for example, significantly greater amounts of fatty acids were absorbed than in control animals fed only with hay (4). With increasing parakeratosis ruminis, however, the absorption capacity decreased noticeably, even below that of the control group (4, 9). The absorption capacity of the ruminal mucosa, however, is influenced not only by its structure, but also by the respective pH of the ingesta (5, 20). If the content of the rumen has a low pH value, acetate, propionate and butyrate are absorbed more rapidly than at a high pH (5, 6, 21, 22). Enzyme complexes located within the ruminal mucosa help to convert a portion of the fatty acids into other metabolic products (20).

The ruminal mucosa, therefore, must be considered a metabolic organ functioning between the contents of the rumen and the bloodstream.

Within the framework of a German-Israeli research project, experiments were carried out to obtain quantitative data about the time necessary for adaptation of the ruminal mucosa to a high or low energy diet. Further investigations were intended to determine the quantitative relationship between the structure of the rumen mucosa and the absorption of short-chain fatty acids.

Methods

1) *Morphological investigations:* Permanent rumen fistulas were surgically created in the seventh month of pregnancy in 9 Israeli-Holstein-Friesian cows from an Israelian Kibbuz. Rumen mucosa biopsies from six places were taken at intervals of one to two weeks during a period from 8/9 weeks ante-partum to 8 weeks post-partum. The samples were evaluated morphometrically as well as by light and electron microscopy. With the beginning of the dry period, the energy content of the ration was drastically reduced. Two weeks prior to calving, the feeding regimen was changed to an energy-rich high lactation diet.

Two 3½ year old non-lactating, non-pregnant Holstein-Friesian cows (I, II) with rumen fistulas were used for experiments in Munich. Both cows were subjected to three feeding periods: 1) energy-poor, 2) energy-rich, and 3) energy-poor, for 7 to 14 weeks each (Fig. 1).

2) Absorption experiments (AE) were carried out with the above two cows at the end of the three feeding periods respectively. The rumen contents were removed and the rumen flushed with water. A plastic tube was inserted into the esophagus via the rumen fistula to prevent inflow of saliva.

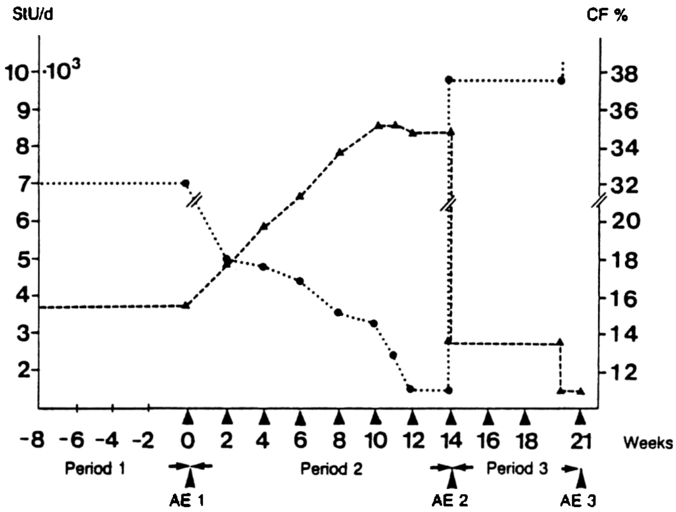
The reticular-omasal orifice was closed by an inflatable plug and 20 liters of a buffered fatty acid mixture were poured into the rumen. Samples were taken every 30 minutes for 4 to 5 hours in order to determine volatile fatty acid (VFA) concentrations.

Detailed descriptions are given by *Liebich* et al., (1982), *Brosi* (1983), *Dirksen* et al., (1984).

Results

Rumen mucosa morphology: As figure 2 shows, a progressive reduction of the ruminal mucosa took place in the Israeli cows when the energy-poor dry period ration was fed. After changing to the high energy diet 14 days prior to calving, intensive proliferation processes began. However, it took 4 to 5 weeks beyond the partus before the mucosa reached their 'full height'.

FIGURE 1. Graphic representation of the supply of starch units (StU) per day —▲— and of the crude fiber (CF —●— (in percent of the dry matter content of the rations) offered in three feeding periods. Cow II. AE = absorption experiment. Arrows below the abscissa = biopsies.



Principally, the same feed and time dependent structural changes of the rumen mucosa were observed in the experiments with the two Munich cows (Fig. 3, 4 5).

Absorption experiments: As can be seen in figure 6 (showing the results of AE 1 and 2 with cow I) the VFA concentrations decreased in AE 2 significantly faster than in AE 1 and AE 3 (not shown).

The difference of absorption capacity is also apparent when the times compared during which the fatty acid concentrations dropped to 50% of the initial values (Table 1, cow II).

Comparing the average VFA quantities absorbed per minute during the first hour (the quantity absorbed in AE 2 = 100%), the differences between AE 2 and AE 1 and AE 3 likewise become evident (Table 2, cow II).

Discussion and Conclusions

The proliferative and reductive processes of the ruminal mucosa represent an adaptive process of the body to high or low VFA concentrations in the ruminal fluid resulting from high or low energy feeding. The purpose of ruminal mucosa growth with energy rich rations is to ensure that the simultaneously increasing VFA quantities are absorbed at the site of their production.

As far as can be seen to date, this adaptation is of significance for two body functions in particular: the stabilization of the pH of the ruminal contents and the energy metabolism.

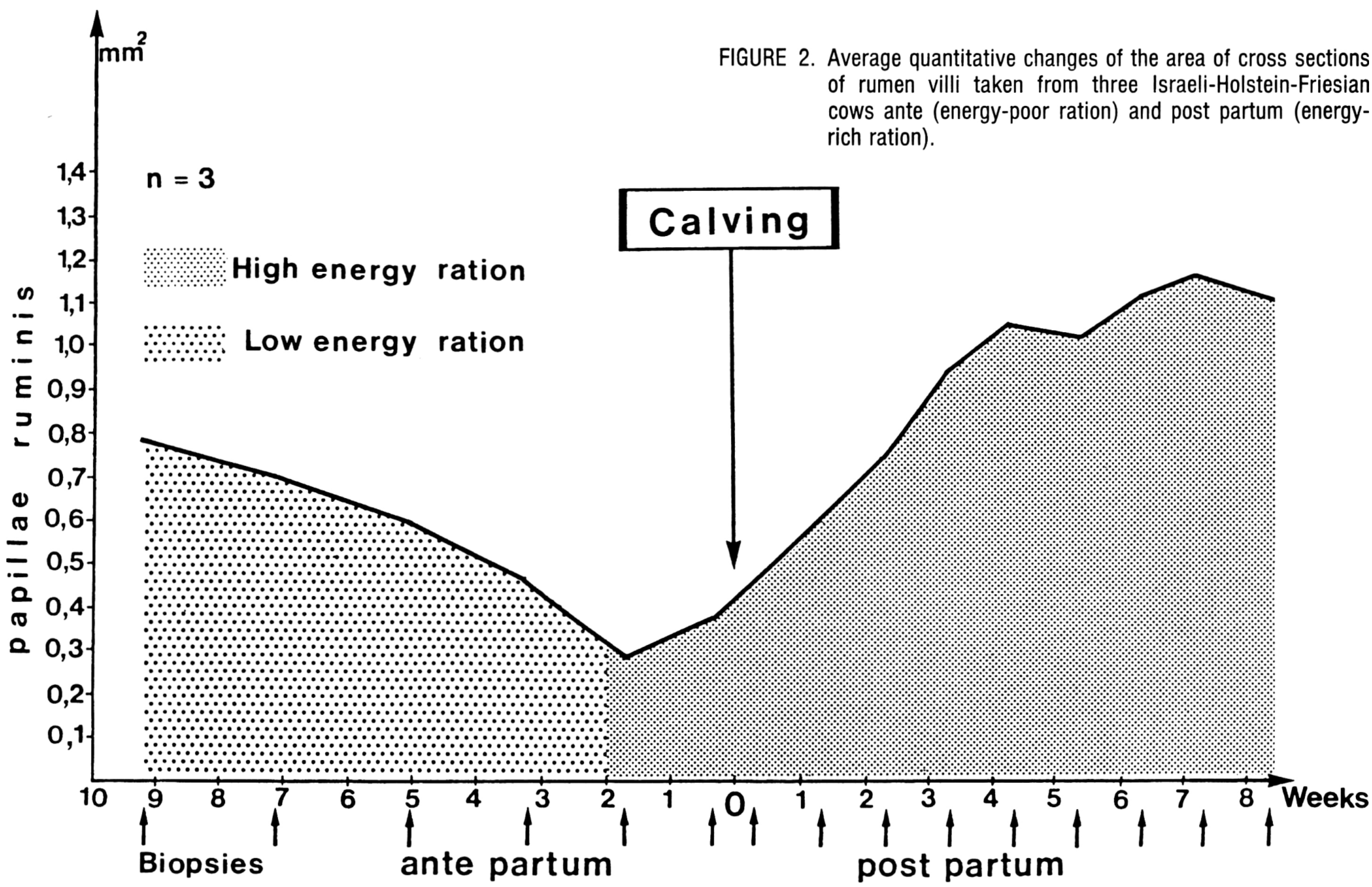
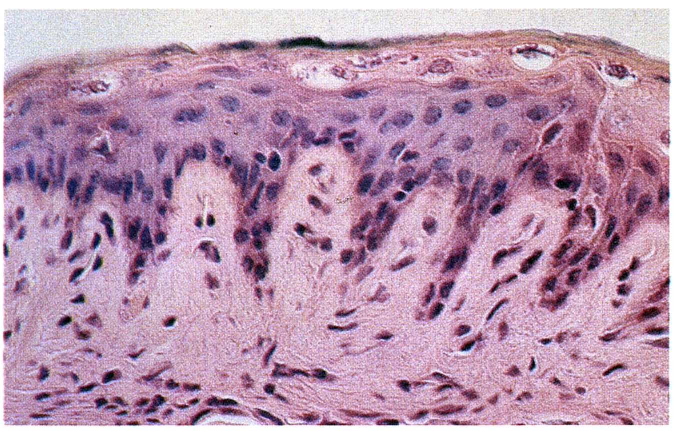


FIGURE 2. Average quantitative changes of the area of cross sections of rumen villi taken from three Israeli-Holstein-Friesian cows ante (energy-poor ration) and post partum (energy-rich ration).

FIGURE 3. Ruminal papillae after feeding a low energy ration (hay) for 7-8 weeks (left) and after a high energy period (right), corresponding to period 1 and 2 in Figure 1.

FIGURE 4. Histological section through the mucosal tissue of a ruminal papilla: top) at the end of feeding period 1 (hay, ad lib.): thin epithelium, short epithelial papillae, poorly developed papillary body; below) at the end of feeding period 2 (energy-rich): thick epithelium, wide and long epithelial papillae, well developed papillary body (enlarged 400x).



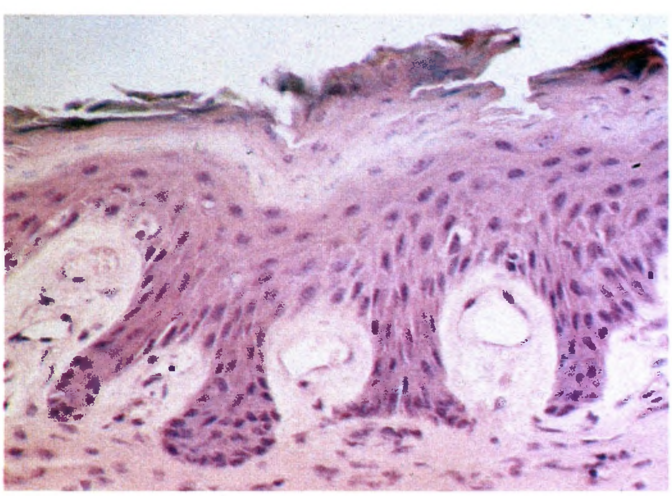
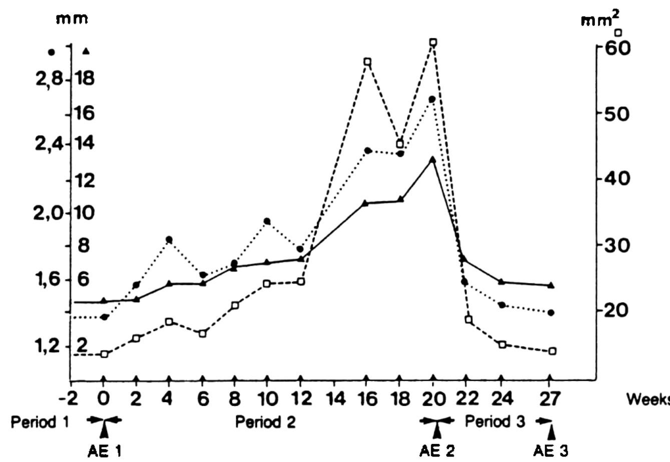


FIGURE 5. Graphic representation of the development of papillae length —▲—, papillae width —●— (mm) and papillae surface area —□— (mm^2) from the end of feeding period 1. Cow I. AE — absorption experiment.



Stabilization of the pH: Increasing amounts of (poorly structured) easily digestible carbohydrates in the ration and simultaneously decreasing (relative and absolute) amounts of well structured roughage result in a reduced secretion of saliva and, therefore, in a lower inflow of buffer substances into the rumen. As the acid production simultaneously increases, the pH value drops. However, as a counter response, the mucosa proliferates and increases the absorption capacity for acids. In our opinion the ruminal mucosa under these conditions becomes the most important organ for the regulation of the pH by preventing the accumulation of acid and in that way a further drop of pH (Fig. 7).

The regulation circle, however, to become effective, requires that the animal be given enough time for the tissues to adapt. On the basis of our present knowledge, it takes 4 to 6 weeks after a change from a low to a high energy ration to achieve a high stabilizing effect. The efficacy, however, increases from week to week (Fig. 8).

FIGURE 6. Change of VFA concentrations (percent of initial values) in absorption experiments 1 and 2 in cow I; A/P/B = Acetic/Propionic/Butyric acid.

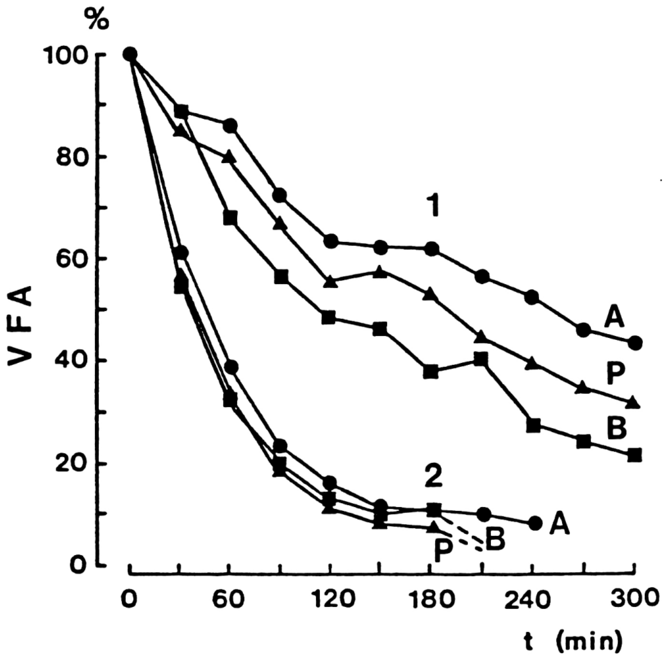


TABLE 1. Time (min.) required for the reduction of the fatty acid concentrations to one half (= 50 %) of the initial concentrations and relative values (absorption experiment 2 = 1.0); cow II.

Cow II	Acetic acid		Propionic acid		Butyric acid	
	min.	relative	min.	relative	min.	relative
AE 1	300	4,8	266	4,9	217	4,3
AE 2	63	1,0	55	1,0	51	1,0
AE 3	200	3,2	147	2,7	110	2,2

It is well known that about 4 weeks are required in the grain feeding beef systems to accustom the cattle to the highly concentrated feed and to avoid rumen acidosis. Until now it was assumed that this period of time is necessary for the adaptation of the ruminal flora. However, we believe that this is, in fact, the time necessary to achieve a sufficient proliferation of the ruminal mucosa.

Energy balance: For the energy metabolism, the significance of the mucosa proliferation is that with increasing absorption capacity, the organism receives increasing amounts of energy supplying fatty acids.

Although fatty acids can also be absorbed at other sites, the absorption from the rumen seems to offer advantages. In addition possible disadvantages resulting from the outflow of larger quantities of acids are prevented.

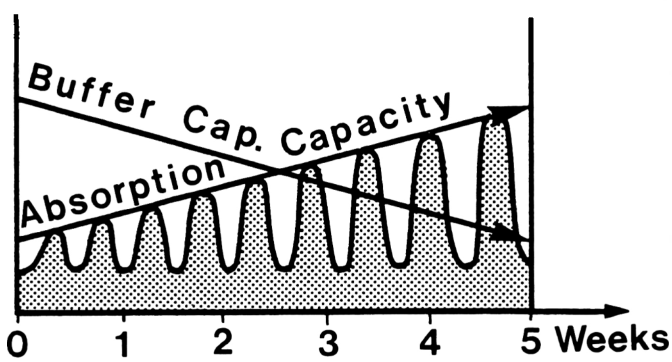
The energy metabolism is also affected via the influence on feed intake. It is not yet clear whether the fatty acid concentration in ruminant blood participates in the regulation of feed intake. It is, however, well known that the feed intake decreases when the pH value drops too far (below 5.5).

TABLE 2. Quantity of fatty acids absorbed per minute during the first hour, with relative values in percent (AE 2 = 100%); cow II.

Cow II	Acetic acid mMol/ min.	%	Propionic acid mMol/ min.	%	Butyric acid mMol/ min.	%	AC + PR + BU mMol/ min.	%.
AE 1	2,7	29	1,2	29	0,9	35	4,8	30
AE 2	9,2	100	4,4	100	2,7	100	16,2	100
AE 3	3,8	42	2,0	47	1,5	57	7,4	46

FIGURE 7. Regulatory processes in the rumen for the stabilization of the pH with an energy-rich diet.

FIGURE 8. Schematic representation of the progressive development of the stabilizing effect of the ruminal mucosa on the pH in the rumen contents.



The results are of particular interest in regard to the energy supply of high producing cows during the first weeks post partum. In order to keep the so called energy gap during peak lactation as small as possible it would be desirable that the ruminal mucosa should be well proliferated at calving. However, to achieve this, it is necessary to commence energy rich feeding as early as 4 weeks prepartum, which would, however, induce an excessive fat deposition with all the well known disadvantages resulting from that. That is the dilemma of the high producing cow!

New methods must, therefore, be sought to induce full development of the ruminal mucosa without providing excessive energy sources during the dry period, perhaps by manipulation of the fatty acid composition, by supplementing with salts of short-chain fatty acids or by other active substances. Future investigations will have to deal with this problem.

Summary

Investigations were carried out to obtain quantitative data about the time necessary for adaptation of the ruminal mucosa to a high or low energy diet. Further studies were intended to determine the quantitative relationship between the structure of the rumen mucosa and the absorption of short-chain fatty acids.

The ruminal mucosa showed progressive reduction when energy-poor rations were fed but intensive proliferation with high energy diets. Adaptation of a "low" ruminal mucosa to a high energy diet took about 4 to 5 weeks. The absorption of acetic, propionic and butyric acid was faster (5 times) and in higher quantity (3 times per minute during the first hour) with 'high' rumen mucosa than with 'low' mucosa. The mucosal adaptation is of major significance for the stabilization of the pH of the rumen contents (with starch and/or sugar rich rations) as well as for energy supply during peak lactation.

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