Advances in intensive ruminant nutrition

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Of the many advances in ruminant nutrition made in recent times the change from dilute roughage-based feeds to highly concentrated grain-rich diets has probably had the greatest single impact on ruminants and on their rate of production. This change has been associated with many new and unexpected nutritional problems. This article deals with the role and uses of the ionophores, the B-vitamins, buffers and branched-chain fatty acids in such concentrated production diets for ruminants. It is evident from this review that intensified animal production and factors such as the use of new drugs, feed additives and recent developments such as the greater use of bypass proteins have an important bearing on the ruminant's requirement for nutrients. There is therefore a need to re-examine established nutrient standards and principles continually as further intensification of ruminant production will influence these requirements and interrelationships in currently unforeseen ways.
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Daar is in die afgelope aantal jare groot vordering gemaak op die gebied van herkouervoeding. Die enkele faktor wat waarskynlik die grootste uitwerking op herkouers en hulle produksietempo gehad het, was die verandering van lae-energie-, ruvoerryke-rantsoene na hoogsgekonsentreerde graanryke-rantsoene. Hierdie verandering het gepaard gegaan met baie nuwe en onvoorsiene voedingsprobleme. Hierdie referaat handel oor die rol en gebruike van die ionofore, B-vitamiene, buffers en vertakteketting-vetsure in sulke gekonsentreerde produksierantsoene vir herkouers. Uit hierdie oorsig is dit duidelik dat intensiewe diereproduksie en faktore soos die gebruik van nuwe medikamente, voerbymiddels en ontwikkelings soos die groter gebruik van verbyvloeiproteïen, 'n belangrike uitwerking het op voedingsbehoeftes van herkouers. Dit is dus nodig om voortdurend bestaande voedingstandaarde en beginsels in heroorweging te neem aangesien verdere intensivering van herkouerproduksie hierdie voedingsbehoeftes en interverwantskappe in tans onvoorsiene maniere sal beïnvloed.
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Advances in the field of ruminant nutrition during recent times have been numerous and involve a wide range of subjects. It is beyond the scope of this review to do justice to the large number developments that have, and continue to enable us to improve the rate and efficiency of meat, milk and wool production from ruminant animals.

Throughout much of this century there has been a tendency towards more intensive feeding of animals which has involved the greater use of concentrated grain-based diets. This swing away from roughage or roughage-rich feeds has gained momentum in recent decades. The widespread use of highly concentrated diets has introduced an entirely new generation of nutritional problems and deficiencies. It is the purpose of this article to concentrate on these specific problems and on the nutritional advances that have followed.

Ionophores

Probably the biggest single impetus given to the feeding of beef cattle and sheep was the discovery that the polyether antibiotics, collectively known as ionophores (Pressman, Harris, Jagger & Johnson, 1967), have such a profound effect on ruminant production. These antibiotics were classified by Pressman, *et al.* (1967) as ionophores because of their ability to complex with mono- and divalent cations and to facilitate their transport and exchange with other cations across a wide variety of biological membranes. It is this ability to disrupt the cation balance of cells to which most, if not all, the biological effects of the ionophores can be attributed (Reed, 1982). Table 1 gives a summary of the biological effects that have been ascribed to monensin, one of the most widely used and studied ionophores (Schelling, 1984). The well-known improvement in efficiency of feedlot gain and better growth of pasture-fed animals appears to be the nett result of these many effects acting in concert. The main areas of ionophore activity in ruminants are their effect on microbial growth, microbial metabolism, nutrient digestibility and nutrient utilization.

Microbial growth

Ionophores improve animal performance by altering the growth of specific bacterial strains favourably. Based on the studies of Chen & Wolin (1979) and Bartley & Nagaraja (1982) lasalocid, for example, has a negative effect on the growth of bacteria which produce lactate or butyrate as a major end-product, and/or produce formate or hydrogen. Bacteria which resist lasalocid are those which produce succinate as a major end-product, ferment or utilize lactate, or produce methane. The increased propionate production not only improves the

Table 1 Biological effects of monensin in the rumen

Item
Greater ruminal propionate concentration
Lower ruminal acetate concentration
Lower ruminal butyrate concentration
Lower ruminal lactate in stressed animals
Higher ruminal pH in stressed animals
Less ruminal methane production
Decreased intake of grain diets
Increased intake of forage diets
Increased ruminal forage fill
Decreased ruminal rate of passage
Increased dry matter digestibility
Increased protein digestibility
Decreased ruminal deamination
Decreased ruminal proteolysis
Protein sparing effect
Modified ruminal escape of protein
Modified ruminal escape of starch
Modified rumen microbial population
Increased body glucose turnover
Modified substrate gluconeogenesis
Reduced 3-methylindole production
Earlier puberty in heifers
Reduced fly pupae in faeces

From: Schelling, G.T., 1984.

efficiency of feed utilization (Chalupa, 1977), but since propionic acid is gluconeogenic it is a more flexible energy source as suggested by Schelling (1984). Also by inhibiting hydrogen and formate production, both of which act as substrates for methane synthesis, methane production is reduced which decreases energy loss. The ionophores are generally bacteriostatic against Gram-positive bacteria while Gram-negative bacteria are usually resistant. This striking difference in sensitivity is due to differences in cell wall structure. This enables the ionophores to penetrate the cell wall of the Gram-positive bacteria more easily and retard their growth (Stuart, 1984).

The effect of lasalocid and monensin in depressing lactate production on the one hand, while on the other hand, not inhibiting the strains which utilize it, explains the action of ionophores in reducing lactic acidosis (Dennis, Nagaraja & Bartley, 1980). Bartley & Nagaraja (1982) also showed lasalocid to be a potent inhibitor of feedlot bloat. All these metabolic processes seem to be the direct result of the effect of ionophores on the growth of specific strains of rumen bacteria.

Modified digestibilities

Research work has been largely concentrated on the effect of ionophores on protein and energy digestibilities. The results have been variable and responses during the adaptation phase are often unfavourable. In general, results in adapted animals indicate that the ionophores give a slight to moderate increase in digestibility of dry matter and/or starch under many conditions (Dinius, Simpson & Marsh, 1976; Rust, Owens, Thornton & Fent, 1978; Poos, Hanson & Klopfenstein, 1979; Beede, Gill, Koenig, Lindsey, Schelling, Mitchell & Tucker, 1980; Ferrell, Gill & Owens, 1982). Increases in nitrogen digestibility in animals fed both low and high protein diets have been reported (Rust, *et al.*, 1978; Joyner, Brown, Fogg & Rossi, 1979; Beede, *et al.*, 1980) while inconsistent results have been reported for urea-containing diets (Dinius, *et al.*, 1976; Poos, *et al.*, 1979). Factors such as feed intake, rumen fill, and rate of passage may influence the results that have been reported.

Protein utilization

A review of the literature strongly suggests that ionophores have a protein sparing effect. This is achieved through the better utilization of feed amino acid nitrogen. Monensin significantly reduces dietary protein breakdown (Schelling, Spires, Mitchell & Tucker, 1977; Van Nevel & Demeyer, 1977; Poos, *et al.*, 1979; Chalupa, 1980), while also decreasing the rate of free amino acid breakdown in the rumen (Schelling, *et al.*, 1977). This decreased deamination is reflected in lower rumen ammonia levels (Dinius, *et al.*, 1976). Monensin thus decreases the bacterial amino acids reaching the abomasum (Poos, *et al.*, 1979) and allows more undegraded feed protein to bypass the rumen (Short, Bryant, Hinds & Fahey, 1978). The nett effect is an increase in the total amount of amino acid nitrogen reaching the abomasum (Owens, Shockey, Fent & Rust, 1978; Poos, *et al.*, 1979) and greater overall nitrogen retention (Beede, *et al.*, 1980).

Ionophore-mineral interactions

The primary mode of action of ionophores is their ability to bind and facilitate the transport of ions through biological membranes. A question which has not yet been widely explored is whether ionophores change the availability and uptake of ions from feedstuffs and from mineral supplements. This question is important in terms of trace elements and particularly for those elements considered to be toxic. The normal uptake, transport and use of divalent minerals in the animal body is accomplished via numerous endogenous 'ionophore' transport routes. The possibility that the exogenous ionophores, lasalocid and monensin, might alter the normal uptake of divalent metal ions has been investigated by Elsasser (1984). In his first experiment with chickens, Fe and Cu in tissues were lower in animals given monensin but higher in those given lasalocid. Ca was lowered in the gut mucosa by both ionophores. In a second experiment, sheep drenched with copper sulphate (100 mg of Cu^{2+}/animal/day), resulted in enhanced Cu accumulation in all animals, with the largest accumulation measured in those fed monensin. These results suggest that adding monensin and lasalocid to diets may change the bioavailability, gut uptake and tissue deposition of divalent minerals, but that the direction in which mineral metabolism is altered is unpredictable. Starnes, Spears, Froetschel & Croom (1984) studied the effect of monensin and lasalocid on the absorption and retention of the major dietary elements. Both ionophores increased apparent absorption of Na, Mg and P and the retention of Mg and P. Serum Zn and Cu concentrations were higher with both ionophores.

The limited data available thus indicate that ionophores alter mineral availability, absorption, transport, and finally, tissue distribution and bioavailability within the cells, of divalent ions.

Potassium

Although potassium (K) is the third most abundant mineral element in the animal body, its supplementation in ruminant diets has, until recently, been considered unnecessary. This is due to the fact that ingredients traditionally used in the feeding of ruminants are good sources of K. With the ever-growing use of grain or grain byproducts, it has become necessary to re-evaluate these previously held views. Increasing recognition has recently been given to the supplementation of K in high-concentrate diets for beef and dairy cattle and sheep feeding.

Beef Cattle and Sheep

Considerable impetus has been given to research on the K requirement of beef cattle by the discovery that the incidence of shipping fever can be alleviated by K supplementation. Feedlot cattle are invariably subjected to varying degrees and periods of stress such as deprivation of water and food and the marketing and transport procedures which precede their entry into feedlots. During this process, considerable dehydration takes place. Water lost by the body is initially lost from the extracellular fluids and is replaced by intracellular water. When this occurs, K concentration increases in the extracellular space and aldosterone is activated to cause excretion of K (Hutcheson, Cole & McLaren, 1984). The nett result is a cellular deficiency of K.

Preston (1980) presented data showing that feedlot lambs and cattle need K supplementation under certain conditions. As a general rule the need of K supplementation increased as roughage level decreased. The optimum level of K for feedlot performance in cattle appeared to be 0,6 – 0,8%. It was also pointed out that under conditions of shipping stress, cattle receiving 1,5% K gained significantly more than cattle receiving diets with 1,0% K. Many research workers have confirmed the need for supplying K at the NRC (1976) recommended level (0,6 – 0,8%) or even at slightly higher levels (Zinn, Owens, Gill & Williams, 1982; Zinn, Owens, Gill, Williams & Lake, 1982; Ferrell, Owens & Gill, 1983; Doran, Owens & Gill, 1984; Hutcheson, *et al.*, 1984) although Kelley & Preston (1984) reported little change in feedlot performance when dietary K ranged from 0,37 to 1,3%.

The conflicting results that have sometimes been reported in the literature can be attributed to the varying conditions under which the many trials have been conducted. Hutcheson, *et al.* (1984) points out that most experiments have been conducted with healthy cattle. This study shows that stressed cattle fed receiving diets containing 1,4% K out-performed control groups receiving only 1,0% K. This work furthermore demonstrates that pre-shipment diets can markedly influence the response to K in the feedlot receiving diet. Cattle pre-fed on 55% concentrate diets showed a much smaller response to K in the subsequent feedlot adaptation period than cattle pre-fed on hay only. Hutcheson, *et al.* (1984) concluded that shipped (i.e. stressed) cattle should receive 24,7 g K/100 kg bodymass for the first 2 weeks after arrival in the feedlot. This is 20% higher than the requirement for non-transported animals.

From the research evidence reviewed, it is obvious that the response to K supplementation will depend not only on the level of K in the basal diet but also on the stage of feeding when the response is monitored and furthermore on the degree of stress to which animals have been subjected. Most studies show that the response to higher K levels is greater during, or is limited to, the early stages of feedlot fattening (Calhoun, Shelton & Linderman, 1974; Zinn, *et al.*, 1982; Ferrell, *et al.*, 1983; Doran, *et al.*, 1984) and that the requirement during the adaptation phase may be higher than the NRC (1976) level (Farlin & Schindler, 1981; Zinn, *et al.*, 1982; Hutcheson, *et al.*, 1984). Finally the pre-shipment diet can influence the magnitude of the subsequent K-response.

Dairy Cattle

As with beef cattle, nutritionists have for a long time taken the K requirement of dairy cows for granted. Factors which have led to a re-evaluation of the need for K supplementation are the increased requirements for K resulting from ever-increasing cow productivity and the greater use of grain or grain byproducts required to meet the demands of such high-producing cows. A further factor requiring a new assessment of K requirements is the finding that heat-stressed cows have a greater requirement for K.

Frank K deficiency symptoms such as a rapid decline in feed and water intake, a rapid drop in milk and blood plasma K levels, loss of vitality, pica, and death are not likely to be seen under farm conditions. In practice, borderline K deficiency causes a loss of appetite and decreases milk production. Early studies (Erdman, Hemken & Bull, 1980; Hemken, 1980) indicated that dairy cows consume more feed and produce more milk when fed higher levels of K than recommended by NRC (1978). From results cited by Jimenez (1983), it is evident that cows producing in excess of 25 kg of milk and consuming normal levels of dry matter may require well in excess of 1% K in the diet. Daniels, Stallcup, Rakes & Lancaster (1984), showed that cows receiving rations containing 1,6% K produced more milk (7430 kg) as compared with those that received 0,8% K (7176 kg) and those receiving 1,2% K (6660 kg).

Heat Stress

University of Florida researchers have investigated the effect of both sodium (Na) and K in diets of shaded and non-shaded dairy cows (Beede, Schneider, Mallonee, Wilcox & Collier, 1984) and have come to the following conclusions. Cows fed K-deficient rations showed greatly decreased milk yield and pica which were rapidly reversed by feeding adequate K (1,1%). Increasing dietary Na from 0,16 to 0,42 to 0,70% increased feed intake and milk yield; increasing K from 1,07 to 1,58% did not influence yield independantly but there was a Na/K interaction with highest yields and best feed conversion being obtained with 0,7% Na and 1,58% K. Increasing K from 0,66% to 1,08% of DM increased yields of shaded and unshaded cows by 6% and 12%, respectively, thus suggesting a beneficial effect with heat stress.

K-Interactions

With increasing recognition being given to K supplementation of highly concentrated cattle diets it should be noted that excessive levels of K, while not toxic, may reduce performance (Jackson, Kromann & Ray, 1971). Recent studies by Greene, Fontenot & Webb (1983) and Greene, Webb & Fontenot (1983) have shed light on how varying K levels may affect the use of magnesium and other minerals. Using four levels of K (0,6; 1,2; 2,4 and 4,8%) and two levels of magnesium (0,1 and 0,2%) they found that increasing K caused a linear increase in faecal magnesium excretion but that the reverse was not true. The largest decrease in magnesium absorption occurred when K levels increased from 1,2 to 4%. Increasing K increased calcium and N absorption but phosphorus absorption was not affected.

B-Vitamins

Until very recently the consensus of opinion amongst nutritionists has been that ruminants with a functional rumen do not require dietary supplies of B-vitamins (NRC, 1978; Maynard, Loosli, Hintz & Warner, 1979; ARC, 1980). The main reason for this belief is the original observation by Theiler, Green & Viljoen (1915) followed by numerous subsequent studies showing that nett B-vitamin synthesis occurs in the rumen. Studies in which B-vitamins have been supplemented, have also given variable results with many studies failing to produce responses while others have produced positive results (Mathison, 1982). In more recent years, the frequency of positive responses to B-vitamins in ruminants subjected to high levels of grain feeding has increased. These responses, together with known cases of specific vitamin deficiencies and with the unknown effect of many modern feed additives on vitamin synthesis and metabolism, call for a re-examination of the role of B-vitamin supplementation of ruminant diets.

Thiamine

Deficiencies of thiamine in cattle, sheep and game have been widely experienced in recent times both overseas and under South African conditions. Most of the interest in thiamine for ruminants involves polioencephalomalacia (PEM) since Davies, Pill, Collings, Venn & Bridges (1965) first demonstrated that thiamine administration cures this affliction. The primary biochemical lesion in PEM appears to be a failure of the brain to obtain energy as glucose. Thus PEM could be produced by hypoglycemia, a primary thiamine deficiency, the inhibition of thiamine requiring enzymes by thiamine analogues, or a combination of these factors.

The most widely held hypothesis on the factors precipitating PEM, is the existence of thiaminase enzymes. Two types of thiaminase have been described (Dixon & Webb, 1964). A thiaminase II which simply cleaves the vitamin yielding thiazole and pyrimidine and thiaminase I which not only destroys the vitamin but also creates a thiamine analogue. The analogue, in the presence of suitable cosubstrates, then inhibits one or more of the thiamine-requiring enzymes necessary for energy metabolism in the central nervous system. Thiaminase I has been obtained from *Clostridium sporogenes, Bacillus thiaminolyticus* and faeces of spontaneous PEM cases (Boyd & Walton, 1977). The preferred cosubstrates from spontaneous PEM cases are aniline, pyridoxine, pyridine, nicotinic acid, histamine and amidazole (Boyd & Walton, 1977). Most of these substances are present in the rumen and histamine appears during lactic acidosis. Brent (1976) has stated that lactic acidosis is often associated with PEM. Nicotinic acid, which is increasingly being recommended as a supplement for dairy cattle, serves as an important thiaminase I cosubstrate and could therefore precipitate PEM. Linklater, Dyson & Morgan (1977) reported that PEM is precipitated by administration of the anthelmintics levamizole hydrochloride or thiabendazole, while Loew & Dunlop (1972) have found that prolonged feeding of amprolium could produce PEM lesions. These compounds act as cosubstrates for thiaminase I (Roberts & Boyd, 1974). In Cuba, Mella, Perez-Olivia & Loew (1974) found that PEM is precipitated by diets of urea and molasses with very low roughage intakes.

If diagnosed early enough, PEM can be treated by large intravenous injections of thiamine. The problem of prevention is, however, more complex. The supplementation of feedlot diets with thiamine is often recommended under practical feedlot situations. Lusby & Brent (1972) prevented PEM in lambs by feeding 150 mg thiamine per day, but PEM developed shortly after thiamine withdrawal. This indicates that, in the presence of thiaminase I, about 1 g thiamine/day would be required to prevent PEM in cattle (Brent & Bartley, 1984). Edwin & Jackman (1982) pointed out that the activity of thiaminase enzymes can be so great as to destroy 1 mg thiamine per min. per kg rumen digesta.

Because such high levels of thiamine are required to compete with the inhibiting analogues, feeding thiamine to prevent PEM does not appear to be very practical. Brent & Bartley (1984) have also warned that high levels of thiamine in the diet will lead to more thiamine circulating and if the concentrations of thiaminase I and cosubstrate are not limiting the rate of thiaminase I reaction, the feeding of thiamine will increase thiamine analogue synthesis and could conceivably precipitate PEM.

Ionophores could play a role in preventing PEM. Miller, Goodrich & Meiske (1983) have found that monensin reduces the ruminal loss of thiamine over extended periods of time. The ionophores also help prevent lactic acidosis and as lactic acidosis is associated with PEM (Brent, 1976), the incidence of this disease might be expected to be reduced by the feeding of ionophores.

Niacin

Niacin can be synthesized by rumen micro-organisms and by the animal from tryptophan. In spite of these sources, recent evidence shows that animals under the stress of high levels of production will respond to supplementary feeding of niacin. From recent reviews by Mathison (1982) and Brent & Bartley (1984) it is evident that although the responses obtained with fattening diets for sheep and beef cattle are variable, most of the studies reviewed show positive responses in terms of gain, efficiency of gain or improved feedlot adaptation. The best level of supplementation appears to be about 100 p.p.m., with 50 p.p.m. being ineffective and 500 p.p.m. producing negative effects (Byers, 1981).

Responses to niacin supplementation in dairy cattle have also been variable but most studies reviewed (Mathison, 1982; Brent, *et al.*, 1984) show positive responses in milk production when niacin is supplemented at a rate of about 6 g per cow per day (250 – 300 p.p.m.). The response is greater in postpartum cows than in mid-lactation and is greater in cows fed natural protein than those fed urea. To prevent ketosis in high-producing cows, as much as 400 p.p.m. of niacin may be required. The greater response to niacin during early lactation is probably largely due to its role in preventing ketosis (Fronk & Schultz, 1979; Brent, *et al.*, 1984).

Various proposals have been put forward as to the mechanisms whereby positive responses to niacin supplementation have been obtained. Niacin's effect on milk production and ketosis in dairy cows can, at least partly, be explained by its effect of increasing blood glucose levels while decreasing plasma or serum concentrations of ketones and free fatty acids (Mathison, 1982). Brent, *et al.* (1984) summarizes evidence which shows that increased milk production in early lactation could be due to niacin providing adequate supplies of pyridine nucleotides for tissue metabolism. Several studies (reviewed by Brent, *et al.* (1984) showed increased microbial protein synthesis and have increased molar proportions of propionate (Arambel, Bartley, Dennis, Riddell, Camac, Higginbotham, Simons & Dayton, 1984). Bacteria can synthesize niacin from tryptophan (Foster & Moat, 1980) but rumen protozoa cannot (Jones, 1974) and must therefore obtain their niacin from bacteria. Brent, *et al.* (1984) postulated that heat treatment of soybean meal would reduce the rumen availability of niacin or tryptophan to bacteria, thus reducing the niacin supply of protozoa. In studies conducted to test this hypothesis, they fed heat-treated and unheated soybean meal with and without niacin. Rumen protozoal numbers were increased when niacin was added to heated, but not when it was added to unheated, soybean meal. Arambel, *et al.* (1984) found that cattle fed unheated soybean meal had higher microbial protein synthesis than with heated soybean meal and that niacin supplementation increased bacterial protein synthesis by 10,9%. It thus appears that niacin is a limiting nutrient when cattle are fed diets containing heated (bypass) soybean protein.

Other B-Vitamins

In the presence of sufficient cobalt, the ruminant, through its micro-organisms, produces and excretes far more vitamin B_{12} than it consumes. On high concentrate diets there is, however, a decrease in vitamin B_{12} synthesis and more analogues are produced than the vitamin itself (Sutton & Elliot, 1972). These natural analogues have little or no vitamin B_{12} activity. In spite of this, there is little evidence in the literature to suggest that growth rate or milk production are enhanced by vitamin B_{12} supplementation. The role of other B-vitamins in ruminant nutrition is reviewed by Mathison (1982) but there is little evidence to date of deficiencies under practical conditions. Gerloff, Herdt, Emery & Wells (1984) have recently studied the effect of inositol deficiency on the occurrence of fatty liver syndrome in dairy cows but the initial studies are inconclusive.

Choline

Although not considered to be a vitamin, choline is often discussed in conjunction with B-vitamins. Choline is synthesized to some degree by animals and is important as a source of biologically active methyl groups. Ruminant researchers are showing increasing interest in choline in view of its possible lipotropic effect in high-producing dairy cows. Atkins, Erdman & Vandersall (1983) and Erdman, Shaver & Vandersall (1984) have demonstrated improvements in butterfat test and slight improvements in feed intake and fat-corrected milk production in cows fed highly concentrated diets supplemented with choline.

Buffers

The use of buffers in ruminant feeds has been widely researched during the past 25 years. The changes in nutritional practice which have led to more intensified interest in buffers during recent times are the much higher levels of grain feeding, the resultant lower roughage intakes, the greater use of milled or pelleted roughage, the more widespread use of silages, and the finer material ensiled due to the use of high speed choppers required for better silage compaction and easier removal from silos. These practices have all led to lower saliva secretion during eating and rumination. One of the major functions of saliva is to provide buffers (sodium and potassium bicarbonates) which neutralize the volatile fatty acids produced during rumen fermentation. Any drop in saliva secretion will be reflected in a more acid rumen. Concentrated diets also have a rapid rate of fermentation and produce higher levels and concentrations of volatile fatty acids. These conditions not only create problems such as clumping of rumen papillae, parakeratosis and liver abscesses but also lactic acidosis during the adaptation period following sudden changes to more concentrated diets. High-grain, low-fibre diets which result in low rumen pH values are, finally, also associated with depressed butterfat percentages in dairy cows.

The response obtained from the feeding of buffers can be expected to be influenced by many factors, such as the kind of buffers in use (sodium bentonite, sodium bicarbonate, potassium bicarbonate, calcium carbonate, dolomitic limestone and magnesium oxide to mention but a few), the levels used the stage of production tested (such as early lactation, feedlot adaptation periods, etc.), the natural buffering capacity of the basal diet, the level of concentrate fed, the kind of animal fed, and whether or not silage is included in the feed.

Buffers in feedlot rations

Variable results have been reported on the value of limestone as a buffer in feedlot situations. Wheeler, Noller & White (1981) found that steers fed 0,7% Ca had higher average gains and more efficient feed conversions than those fed diets containing 0,35% Ca. In these experiments, feeding of $NaHCO_3$ (1,5%) in addition to $CaCO_3$ (0,75%) had either no effect or reduced animal performance at a level of 1,5%. Varner & Woods (1972) found that increasing Ca from 0,20 to 0,41% with limestone, significantly improved steer performance but that a further increase to 0,50% Ca (0,83% limestone) did not significantly improve performance of steers fed on 85% concentrate diets. Brink, Turgeon, Harmon, Steele, Mader & Britton (1984) fed diets containing 80 – 85% whole, rolled or high-moisture maize to beef weaners. In one experiment, steers fed high moisture maize-based diets with 1,7% limestone were significantly more efficient than those fed 0,8% limestone. In the other three experiments the higher levels of limestone consistently improved efficiency of gain although the differences were not statistically significant. El Tayeb, Galyean & Kiesling (1984) fed 75% concentrate diets supplemented with 0,6; 1,5 and 3% limestone (0,6; 1,2 and 1,7% dietary Ca) and found that dry matter intake increased linearly with limestone. Owens, Goetsch, Weakley & Zinn (1983) reviewed the results of 40 comparisons and concluded that limestone, on the average, improved gain by 0,9%, efficiency by 2,2%, and reduced feed intake by 1,3%. Improvement in efficiency was greatest when the unsupplemented diet contained less than 0,35% calcium.

In contrast to these predominantly favourable results, Russel, Young & Jorgensen (1980) found that supplementing a 88% whole maize diet with 1,8% limestone resulted in poorer feed intakes, gains and efficiencies than was the case with steers fed a control diet containing 0,4% limestone.

Several studies have shown that the fineness with which limestone is ground influences its rate of reactivity and can therefore have an effect on its buffering ability, efficiency of animal performance, and level of limestone required for optimum animal production (Brink, *et al.*, 1984; Nocek, Braund & English, 1983).

Sodium bicarbonate ($NaHCO_3$), sodium bentonite, and other buffers have also been extensively tested in lamb and beef cattle production trials. In recently reported trials, Thomas & Hall (1984) attempted to explain the extremely variable results of earlier experiments by comparing a control diet with 2 levels (1 and 2,5%) of $NaHCO_3$ and sodium pyrophosphate ($Na_4P_2O_7$) in both high-concentrate and high-roughage diets fed to cattle. With the high-concentrate diets, both buffers tended to increase feed intakes while bodymass gains were significantly (14%) improved by the 1% ($Na_4P_2O_7$) supplementation. Both buffers at the 1% level and ($Na_7P_2O_4$) at the 2,5% level also significantly improved feed conversion efficiencies. On the high-roughage diets, however, feed intake, livemass gains and efficiency of feed conversion were all better on the non-buffered control diets. Calhoun, *et al.* (1974) reported the results of two experiments in which buffers ($KHCO_3$ and $Ca(OH)_2$) improved gains and feed efficiencies of lambs fed high-concentrate diets but only during the first 28-day period of their feeding trials. Feeding buffers after the lambs were adapted had no advantage. Improved adaptation in feedlot lambs has also been reported by Colling & Britton (1975). These results were confirmed in experiments reported by Huntington, Emerick & Embry (1977) who found that lambs on high-concentrate diets supplemented with 2 and 4% bentonite or 2% $NaHCO_3$ adapted more rapidly as was evident from (non-significant) better mass gains during the initial 21-day period. Only the lower level of each buffer improved efficiency of gain during this period. Over the entire 86-day feeding period there were, however, no significant improvements, with the higher levels of buffers reducing the rate of gain overall. Of practical importance was the fact that 19% of the lambs fed $NaHCO_3$ died as a result of, or had non obstructive urinary calculi. Nine lambs also died as a result of polioencephalomalacia, seven of which were fed 4% bentonite. An increased incidence of urinary calculi in steers has also been reported by Emerick, Embry & Dunn (1977) with a 61% incidence of urinary mineral deposits in steers fed $NaHCO_3$ versus only a 40% incidence in control steers. These results suggest that the formation of urinary deposits could be precipitated by the increased alkalinity of urine which would be expected from the use of dietary buffers. Russel, *et al.* (1980) found that both 1,8% limestone and 0,9% $NaHCO_3$ fed singly and particularly when fed in combination, reduced feed intake, mass gains and feed efficiencies.

Kellaway, Grant & Hargreave (1976) conducted two trials using 2% of either $NaHCO_3$ or Na_2HPO_4. Feed intake and gain in calves were higher with than without extra buffer salts. From the second trial, designed to separate the sodium effect they suggested that the response to buffers in their earlier work was due to Na rather than the buffer anions.

Buffers in dairy cows

Erdman, *et al.* (1980) demonstrated that increasing calcium above the NRC (1978) requirement of 0,5% to 1,03% significantly increased feed intake by 1,3 kg or, expressed as a percentage of bodymass, from 3,47% to 3,78%. Rogers, Davis & Clark (1982) showed that the addition of 2,4% limestone to a 75% concentrate: 25% maize silage diet, reduced dry matter intake with no effect on milk production. Limestone thus increased efficiency of milk synthesis when compared with basal diets containing $NaHCO_3$ alone or in combination with limestone. Nocek, *et al.* (1983) compared 0,77% and 1,15% calcium and similarly found that the higher level of calcium depressed feed intake but increased milk production efficiency of dairy cows. Kincaid, Hillers & Cronrath (1981) were, however, unable to demonstrate any difference in feed intake, milk production or feed efficiency between cows fed either 1,0% or 1,8% calcium in the total daily ration (DM basis).

Much attention has been devoted to measuring the effect of $NaHCO_3$ on feed intake and milk plus butterfat production, during early lactation in particular. There is much evidence to prove that $NaHCO_3$ will help prevent milk fat depression on high-concentrate, low-roughage diets (Emery & Brown, 1961; Emery, Brown & Bell, 1965; Emery, Brown & Thomas, 1964; Miller, Hemken, Waldo, Okamoto & Moore, 1965; Thomas & Emery, 1969a & b; Erdman, Botts, Hemken & Bull, 1980; Edwards & Poole, 1983). The use of buffers has, however, sometimes resulted in reduced feed palatability and lower concentrate intakes (Emery, *et al.*, 1964; Emery, *et al.*, 1965; Thomas & Emery, 1969a; Stout, Bush & Morrison, 1972), although others have found the opposite (Erdman, *et al.*, 1980). Erdman, Douglass, Hemken, Teh & Mann (1982) argued that many of these experiments were short-term and that the buffers were introduced suddenly. They therefore set about comparing the sudden versus gradual inclusion of 1,5% $NaHCO_3$ in dairy concentrates. They concluded that the sudden introduction of 1,5% $NaHCO_3$ reduced concentrate intake during the week 1 and 2 by 0,7 and 0,9 kg/day whereas a gradual increase prevented this drop. Eating rate was also unaffected by the gradual addition of $NaHCO_3$. Gradual introduction of $NaHCO_3$ increased milk fat by 0,5%. Milk production was depressed 0,7 to 1,6 kg/day by both sudden and gradual $NaHCO_3$ addition during weeks 1 and 2, but declines were temporary and differences at the end of the trial were small.

Several studies have shown that cows fed buffered rations reach peak production 2 – 3 weeks earlier than those fed unbuffered rations (Erdman, *et al.*, 1980). Kilmer, Muller & Wangsness (1980) indicated a positive response during early lactation to 0,7% $NaHCO_3$ in the total daily ration of maize silage (60%) and concentrate (40%) with cows peaking earlier. Chase, Chalupa, Hemken, Muller, Kronfeld, Lane, Sniffen & Snyder (1982) compared 0; 0,4; 0,8 or 1,6% $NaHCO_3$ in the total daily dry ration but found no differences in milk production and dry matter intake but those receiving 1,6% $NaHCO_3$ had higher actual milk fat percentages. English, Fronk, Braund & Nocek (1983) were also unable to demonstrate advantages in using 1,5% $NaHCO_3$ or 0,5% MgO on daily dry matter intake, bodymass loss and milk yield or composition during the first 8 weeks of lactation.

Buffers in calf starter rations

The inclusion of $NaHCO_3$ in calf starter rations has generally resulted in improved feed consumption, mass gains and overall animal performance. Sodium bicarbonate fed at levels from 2 to 9% to both pre- and post-weaned calves generally improved animal response with 2 – 6% $NaHCO_3$ appearing to be optimum (Kang & Leibholz, 1973; Kellaway, Grant & Chudleigh, 1973; Kellaway, *et al.*, 1976; Kellaway, Thompson, Beever & Osborne, 1977; Okeke & Buchanan-Smith, 1982). In contrast, other workers have reported no effect on feed intake and growth of calves fed $NaHCO_3$ (Wheeler, Wangsness, Muller & Griel, 1980; Hart & Polan, 1984).
& Polan, 1984).

Branched-chain fatty acids

Branched-chain fatty acids (isobutyric, isovaleric and 2-methylbutyric) and the straight-chain acid, valeric, are essential bacterial nutrients and enchance the growth of cellulytic bacteria (Bryant & Robinson, 1962; Slyter & Weaver, 1969; Bryant, 1973). Isobutyric, isovaleric and 2-methylbutyric acids are produced in the rumen mainly by oxidative deamination and decarboxylation of the amino acids, valine, leucine and isoleucine, respectively (Allison & Bryant, 1963), while valeric acid is produced mainly from carbohydrate or amino acids such as proline (Dehority, Johnson, Bentley & Moxon, 1958). In the majority of trials involving these acids one or more of the following characteristics were improved: feed intake, cellulose digestion, nitrogen retention, microbial growth and mass gains (Hemsley & Moir, 1963; Kay & Phillipson, 1964; Cline, Garrigus & Hatfield, 1966; Van Gylswyk, 1970; Umunna, Klopfenstein & Woods, 1975; Soofi, Fahey, Berger & Hinds, 1982; Russell & Sniffen, 1984).

The earlier studies on the effect of these acids on animal production involved mainly steers, growing heifers and sheep usually fed high-cellulose, urea diets. The emphasis of earlier studies was also to investigate single or limited combinations of these acids on production and rumen metabolism. Research work on dairy cattle fed normal production rations has only recently been conducted.

Research work by Felix, Cook & Huber (1980 a,b) suggested that mixtures of C4 and C5 branched-chain fatty acids plus valeric acid improved nitrogen retention, milk yield, and persistancy of milk yield of dairy cows fed diets containing urea, maize silage and maize grains. These results were confirmed by a recent three-university trial (Table 2) in which the effect of ammonium salts of branched fatty acids (AS-VFA)

Table 2 Effect of isoacids on milk yield and feed intake, three-university average

Measurement	Control	Isoacids
Total feed intake (kg DM)		
Calving to 105 days	18,4	19,1
106 – 210 days	17,5	17,3
305-day lactation	17,3	17,5
4% fat-corrected milk yield		
Calving to 105 days	27,2	29,4
106 – 210 days	20,3	21,4
305-day lactation	19,7	21,6

(Adapted from: Papas, *et al.*, 1984)

on dairy cows over a full lactation were investigated (Papas, Ames, Cook, Sniffen, Polan & Chase, 1984). AS-VFA consisted of a mixture of three C-5 volatile fatty acids namely isovaleric, 2-methylbutyric and valeric acids and ammonium isobutyrate fed at various blends. Cows receiving the optimum blend peaked higher, produced more milk and more 4% fat-corrected milk, milk protein and total solids than control cows. Sweeney, Peirce-Sandner, Papas, Rogers, Cummins, Conrad & Muller (1984) concluded that the ammonium salts of branched-chain fatty acids increased milk and fat-corrected milk yields in four out of five diets tested.

It is evident from the foregoing that the branched fatty acids not only limit bacterial growth on urea-cellulose rich diets but are also of importance in rations for high-producing dairy cows. Because rumen bacteria derive these essential growth factors from amino acids they are likely to become more important as the amount of fermentable carbohydrate in diets is increased and under conditions where rumen undegradable or bypass protein is increased.

The American Food and Drug Administration has recently approved a petition sought by Eastman Chemical Products Inc., allowing the use of a dairy cow supplement containing a blend of calcium and ammonium salts of the 5-carbon acids; isovaleric, 2-methylbutyric and *n*-valeric acids, which they claim will boost average milk yields by 5 – 6 lb/cow/day (Feedstuffs, 1984).

From this review it can be concluded that the intensification of ruminant production and the use of feed additives have resulted in the modification of previously accepted nutritional requirements. If rate of production and intensification of ruminant production continue to increase in future years it will be necessary to re-examine and adapt nutritional standards continually in currently unforeseen ways.

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