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Invited review: Use of butyrate to promote gastrointestinal tract development in calves

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ABSTRACT

Promotion of microbial butyrate production in the reticulorumen is a widely used method for enhancing forestomach development in calves. Additional acceleration of gastrointestinal tract (GIT) development, both the forestomach and lower parts of the GIT (e.g., abomasum, intestine, and also pancreas), can be obtained by dietary butyrate supplementation. For this purpose, different sources (e.g., butyrate salts or butyrins), forms (e.g., protected or unprotected), methods (e.g., in liquid feed or solid feed), and periods (e.g., before or after weaning) of butyrate administration can be used. The aim of this paper was to summarize the knowledge in the field of butyrate supplementation in feeds for newborn calves in practical situations, and to suggest directions of future studies. It has been repeatedly shown that supplementation of unprotected salts of butyrate (primarily sodium salt) in milk replacer (MR) stimulates the rumen, small intestine, and pancreas development in calves, with a supplementation level equating to 0.3% of dry matter being sufficient to exert the desired effect on both GIT development and growth performance. On the other hand, the effect of unprotected butyrins and protected forms of butyrate supplementation in MR has not been extensively investigated, and few studies have documented the effect of butyrate addition into whole milk (WM), with those available focusing mainly on the growth performance of animals. Protected butyrate supplementation at a low level (0.3% of protected product in DM) in solid feed was shown to have a potential to enhance GIT development and performance of calves fed MR during the preweaning period. Justification of this form of butyrate supplementation in solid feed when calves are fed WM or after weaning needs to be documented. After weaning, inclusion of unprotected butyrate salts in solid feed was shown to increase solid feed intake, but the effect on GIT development and function has not been determined in detail, and optimal levels of supplementation are also difficult to recommend based on available reports. Future studies should focus on comparing different sources (e.g., salts vs. esters), forms (e.g., protected vs. unprotected), and doses of supplemental butyrate in liquid feeds and solid feeds and their effect not only on the development of rumen, abomasum, and small intestine but also the omasum and large intestine. Furthermore, the most effective source, form, and dose of supplemental butyrate in solid feed depending on the liquid feed program (e.g., MR or WM), stage of rearing (e.g., pre- or postweaning), and solid composition (e.g., lack or presence of forage in the diet) need to be determined.
Key words: feed additive, rumen, small intestine, maturation

INTRODUCTION

The gastrointestinal tract (**GIT**) of calves is not fully developed at birth. In particular, the forestomach is underdeveloped and not prepared for solid feed digestion (Heinrichs, 2005). Substantial development of the forestomach can be obtained even within the first 3 to 4 wk of postnatal life (Klein et al., 1987; Quigley et al., 1991; Heinrichs, 2005) that results in willing intake and efficient solid feed digestion at a very early age (Hill et al., 2010). However, the development of the forestomach usually proceeds for at least several months (Bailey, 1986; Vazquez-Anon et al., 1993), and the preweaning development may affect the performance and productivity of the animals later on (Khan et al., 2016). Besides the forestomach, in the first weeks of a calf′s life, substantial developmental changes are observed in other parts of the GIT, namely the abomasum and small intestine (Guilloteau et al., 2009a; Flaga et al., 2011). These are apparent predominantly in the first

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2 to 3 wk after birth, before the rumen development (Guilloteau et al., 2009a). Furthermore, the first few weeks of a calf′s life are a period of extensive pancreatic function development (Biernat et al., 1999; Zabielski et al., 1999; Zabielski et al., 2002). As opposed to the forestomach, the development and maturation of the abomasum, small intestine, and pancreas have an enormous effect not only on solid feed digestion but also on liquid feed digestion [milk or milk replacer (**MR**)], a main source of nutrients for the newborn calf before the initiation of solid feed intake (Guilloteau et al., 2009b; Górka et al., 2011b).

Because GIT development affects feed intake, efficiency of digestion, and resistance to gastrointestinal disorders, and thus animal growth and health, each method enhancing these processes is highly desirable. In newborn calves, as well as in ruminants in general, promotion of ruminal butyrate production is known to accelerate ruminal epithelium growth and maturation (Sakata and Tamate, 1978; Mentschel et al., 2001). Intraruminal butyrate infusion or intake of feeds high in starch and sugars, which promotes ruminal butyrate production, results in longer ruminal papillae and, likely, a higher surface area for nutrient absorption (Sakata and Tamate, 1978; Mentschel et al., 2001; Lesmeister and Heinrichs, 2005). Therefore, nutritional strategies aiming to stimulate forestomach development in calves are widely used in practice (Heinrichs, 2005; Lesmeister and Heinrichs, 2005; Khan et al., 2016).

It has been shown in numerous studies that substantial acceleration of GIT development in calves can be obtained by dietary butyrate supplementation (Guilloteau et al., 2009b; Górka et al., 2011a,b), as in pig neonates (Kotunia et al., 2004; Le Gall et al., 2009). This effect was not limited to the rumen as butyrate was proved to be an efficient stimulator of the development of abomasum, small intestine, and pancreas in calves (Guilloteau et al., 2009b; Górka et al., 2011a, 2014). Aforementioned reports have been applied in practical nutrition of newborn calves, by proposing commercial feed additives containing butyrate (Hill et al., 2011a,b, 2016). The aim of this paper was to summarize the knowledge in the field of dietary butyrate use to promote GIT development in calves and to suggest directions of future studies.

SOURCES OF BUTYRATE AND ITS IMPORTANCE FOR THE GIT

Butyrate is short-chain fatty acid (**SCFA**) and one of the major end products of bacterial carbohydrate fermentation in the forestomach and large intestine (Bergman, 1990). Of the 3 major SCFA produced in the GIT in the largest quantities (acetate, propionate, and butyrate), butyrate is the least abundant but behaves the most dynamically (Ploger et al., 2012). Depending on the diet composition, its molar proportion in total fermentation acids may range from 5 to over 20% (Ploger et al., 2012). In consequence, its production in the GIT can be modulated to a great extent. Butyrate is also naturally present in milk and dairy products (Guilloteau et al., 2010a) and can be supplemented in feed as butyrate salts (calcium, sodium, potassium, or magnesium) or butyrins (esters of butyrate and glycerol, i.e., mono-, di-, or tributyrin; Moquet et al., 2016). In this paper, to simplify the text, the term “butyrate” will be used interchangeably for acid, anion, salt, and ester forms, and a particular one will be specified and discussed only when necessary. Furthermore, the term “protected” or “unprotected,” respectively, will be used for butyrate embedded or not embedded in the continuous lipid matrix, as proposed by Moquet et al. (2016).

Intake with Milk

Prior to the rumen development, butyrate present in milk is the main source of this molecule for the newborn calf. Although free butyrate concentration in whole milk (**WM**) is relatively low (0.16 g/L in cow’s milk), it may be sufficient to affect GIT development and function (Guilloteau et al., 2010a). Furthermore, in newborn ruminants butyrate is released from milk fat in the abomasum as a result of pregastric lipase action (Drackley, 2008). Bovine milk fat contains 2 to 4% of butyrate (Palmquist et al., 1993; Chilliard et al., 2009), resulting in overall butyrate content in DM of WM even greater than 1%. As a result, a calf consuming 8 L of milk/d (≈1 kg of DM) consumes up to 10 g of butyrate/d. In milk fat, butyrate is located at the third position of triacylglycerols, which is a place of pregastric lipase action (Drackley, 2008). Although the amount of butyrate released from milk fat in the abomasum is difficult to assess, it may play an important physiological role (Drackley, 2008; Guilloteau et al., 2010a). To support this hypothesis, butyrate supplemented in MR stimulated the rumen, abomasum, small intestine, and pancreas development in newborn calves (Guilloteau et al., 2009b; Górka et al., 2011b, 2014) and its delivery in MR, even at a very small dose (0.3% of DM), was sufficient to modulate GIT secretion of gut regulatory peptides and hormones (Guilloteau et al., 2009b).

Production in the Rumen

Microbial fermentation of carbohydrates in the rumen is the most important source of butyrate for ruminants (Bergman, 1990). In dairy cows, depending on the stage of lactation and diet composition, its daily