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Short communication: Interrelationship between butyrate and glucose supply on butyrate and glucose oxidation by ruminal epithelial preparations

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ABSTRACT

The aim of this study was to determine whether dietary Na-butyrate supplementation affects butyrate and glucose oxidation by ruminal epithelial preparations and whether this effect can be acutely modulated by substrate (glucose and butyrate) supply. Eighteen Suffolk wether lambs (6 lambs/treatment) were blocked by body weight and, within block, randomly assigned to the control treatment (CON) or to diets containing differing Na-butyrate inclusion rates (1.58 or 3.16%) equating to 1.25 (B1.25), and 2.50% (B2.50) butyrate on a dry matter basis, respectively. All lambs received their diet for a period of 14 d. After dietary adaptation, lambs were killed and the ruminal epithelium was harvested from the ventral sac, minced finely, and used for in vitro incubations. Incubation medium contained either a constant concentration of glucose (4 m*M*) with increasing butyrate concentrations (0, 5, 15, 25, or 40 m*M*) or a constant butyrate concentration (15 m*M*) with increasing glucose concentrations (0, 1, 2, 4, or 8 m*M*) to allow for the evaluation of whether acute changes in the concentration of metabolic substrates affect the oxidation of glucose and butyrate. We observed no interactions between the in vivo and in vitro treatments. Increasing dietary butyrate supplementation linearly decreased glucose oxidation by ruminal epithelial preparations, but had no effect on butyrate oxidation. Increasing butyrate concentration in vitro decreased (cubic effect) glucose oxidation when butyrate concentration ranged between 5 and 15 m*M*; however, glucose oxidation was increased with a butyrate concentration of 40 m*M*. Butyrate oxidation decreased (cubic effect) as glucose concentration increased from 1 to 4 m*M*; however, butyrate oxidation increased when glucose was included at 8 m*M*. The results of this study demonstrate that dietary butyrate supplementation can decrease glucose oxidation by the ruminal epithelium, but the relative supply of glucose and butyrate has a pronounced effect on substrate oxidation.
Key words: butyrate, glucose, ruminal epithelium, oxidation

Short Communication

The use of butyrate as a dietary supplement has received considerable interest in recent years (Guilloteau et al., 2009; Górka et al., 2011). Butyrate is considered to be the preferred energy substrate for ruminal epithelial cells. This is based on low portal recovery of butyrate compared with acetate and propionate when these short-chain fatty acids (**SCFA**) were infused into the washed reticulorumen (Kristensen et al., 2000a; Kristensen and Harmon, 2004a) and an inhibitory effect of butyrate on acetate and propionate activation and metabolism, at least in vitro (Ash and Baird, 1973; Harmon et al., 1991).

Intensive and preferential metabolism of butyrate over other SCFA by the ruminal epithelium has been reported in many in vivo and in vitro studies (Weigand et al., 1975; Kristensen et al., 2000a; Kristensen and Harmon, 2004a) and it is estimated that between 25 and 80% of the butyrate absorbed by the ruminal epithelium is metabolized to ketone bodies (Weigand et al., 1972; Kristensen et al., 2000b). However, ketogenesis does not contribute substantially to the cellular ATP supply (Kristensen and Harmon, 2004b). Extensive use of butyrate for ketogenesis and the low ATP yield arising from ketogenesis indicate that a substantial portion of the intracellular energy supply must be obtained from the oxidation of other substrates. Harmon (1986) showed that although butyrate decreases glucose uptake by rumen epithelium in vitro, glucose oxidation was not changed. Furthermore, Harmon (1986) and El-Kadi et al. (2009) observed an increase in glucose oxidation and lactate production from glucose by the ruminal epithelium when animals were fed high-concentrate diets. These data suggest that dietary fermentability and perhaps butyrate supply may alter butyrate and glucose oxidation by the ruminal epithelium.

This study aimed to determine whether dietary butyrate supplementation alters glucose and butyrate

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oxidation by the rumen epithelium and whether acute changes in substrate availability modulate substrate oxidation.

The study was conducted at the University of Saskatchewan and all experimental procedures involving animals were reviewed and approved by the University of Saskatchewan Animal Research Ethics Board (Protocol no. 20100021) before initiation of the study.

A detailed description of the study design has been published (Wilson et al., 2012). Briefly, 18 Suffolk wether lambs with an average initial BW of (mean ± SD) 47.4 ± 1.4 kg were provided 7 d to adapt to the housing (2.25-m^2 pens with rubber mats) and dietary conditions before starting the study. To ensure that DMI did not confound the results, lambs were stratified by BW and, within strata, assigned to 1 of 3 treatment diets with the amount of feed offered restricted to 3% of BW on a DM basis. The ingredient composition (% of DM) of the diets consisted of barley silage (10), and a supplemental pellet (90) for the control treatment (**CON**). To provide dietary butyrate at 1.25 (**B1.25**) and 2.50% (**B2.50**) on a DM basis, the supplement pellet was partially replaced (1:1 ratio) by Na-butyrate (Sigma Aldrich, St. Louis, MO) equating to dietary Na-butyrate inclusion rates of 1.58 and 3.16% (DM basis). The entire dose of the Na-butyrate was mixed with one-half of the silage allocation and offered at 0830 h, with the remaining portion of the diet being offered at 1030 h. This feeding strategy ensured that the whole dose of butyrate was consumed before feeding the remaining diet allocation. A similar feeding strategy was applied to CON lambs except that they only received an equal proportion of barley silage. All lambs received their treatments for 14 d, which was deemed to be a sufficient amount of time, as marked changes in functional activity of the ruminal epithelium can be observed within 7 d (Etschmann et al., 2009).

Lambs were killed at 1000 h, after receiving their initial feeding (0830 h feeding only), via captive bolt stunning and exsanguination. A 100-cm^2 piece of ruminal tissue was harvested from the ventral sac and the epithelium was gently separated from the underlying tissues. Epithelial sheets were washed and transported to the laboratory (for details, see Wilson et al., 2012). In the laboratory, the ruminal epithelium was blotted dry and minced finely. Approximately 250 mg (exact weight recorded) of tissue was placed in 25-mL Erlenmeyer flasks following the protocol described by Harmon et al. (1991) with minor modifications. To each flask, 2.75 mL of oxygenated buffer (pH 7.4 and 39°C; Table 1) containing either glucose (4 m*M*) or butyrate (15 m*M*) was added to determine glucose and butyrate oxidation, respectively. Furthermore, for the measurement of glucose oxidation, solutions containing 0, 55, 165, 275, and 440 m*M* butyrate were prepared and spiked with D-[^{14}C(U)]-glucose (11.8 GBq/mmol, PerkinElmer Inc., Woodbridge, ON, Canada). The respective radiolabeled stock solution (252.4 μL) was then added to Erlenmeyer flasks (in triplicate) to achieve final butyrate concentrations of 0, 5, 15, 25, or 40 m*M*, and 9 kBq of ^{14}C-glucose with a final glucose concentration of 4 m*M*. For measurement of butyrate oxidation, solutions containing 0, 11, 22, 44, and 88 m*M* glucose were prepared and spiked with [1-^{14}C]-butyrate (2.0 GBq/mmol, Moravek Biochemicals, Brea, CA). The radiolabeled stock solution (252.4 μL) was then added to Erlenmeyer flasks (in triplicate) to achieve final glucose concentrations of 0, 1, 2, 4, or 8 m*M*, and 9 kBq of ^{14}C-butyrate, achieving a final butyrate concentration of 15 m*M* in all flasks. This design allowed us to evaluate whether increasing the concentration of glucose affects butyrate oxidation by ruminal epithelial preparations, and vice versa. The ranges of glucose and butyrate concentrations used were chosen to cover and extend beyond the ranges observed for plasma glucose and ruminal butyrate, respectively.

After radiolabeled stock solutions were added, the Erlenmeyer flasks were sealed with rubber stopper tops (model number 882310, Kimble Chase Life Science and Research Products LLC, Vineland, NJ) that were fitted with disposable center wells (part 882320, Kimble Chase Life Science and Research Products LLC). Flasks were placed in a shaking water bath (45 rpm/min at 39°C) and incubated for 1 h, which was within the linear range of CO_2 production measured in validation incubations before the start of the study and that reported by Harmon et al. (1991). In addition, triplicate flasks were prepared as blanks. Blanks were prepared in the same manner as all other flasks except they were not spiked with ^{14}C-glucose or ^{14}C-butyrate. Blanks were terminated at the start of the 1-h incubation period and were used to correct for background

Table 1. Chemical composition (m*M*) of experimental buffers[1]

Chemical	Glucose oxidation	Butyrate oxidation
$CaCl_2$	2	2
$MgCl_2$	1	1
Na_2HPO_4	2	2
NaH_2PO_4	1	1
KCl	5	5
NaCl	30	30
Na-gluconate	45	45
HEPES	15	15
$NaHCO_3$	25	25
Glucose	4	
Na-butyrate		15

[1]Buffers contained penicillin G (60 mg/L), kanamycin sulfate (100 mg/L), and flurocytosine (50 mg/L).

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