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Effect of increasing the proportion of dietary concentrate on gastrointestinal tract measurements and brush border enzyme activity in Holstein steers

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ABSTRACT

The aim of this study was to determine the time course for adaptation of the reticulo-rumen, omasum, abomasum, and small intestine in response to an abrupt increase in the proportion of grain in the diet. Adaptive responses include tissue and digesta mass, small intestinal length, and brush border enzyme activity in the duodenum, proximal jejunum, and ileum. Twenty-five Holstein steers (213 ± 23 kg; 5 to 7 mo of age) were blocked by body weight, and within block were randomly assigned to 1 of 5 treatments: the control diet (CTRL; 92% chopped grass hay and 8% mineral and vitamin supplement on a dry matter basis) or a moderate grain diet (MGD; 50% chopped grass hay, 42% rolled barley grain, and 8% mineral and vitamin supplement) that was fed for 3 (MGD3), 7 (MGD7), 14 (MGD14), or 21 d (MGD21). Dry matter intake was limited to 2.25% of body weight to ensure that changes in dry matter intake did not confound the results. On the last day of the dietary exposure, steers were slaughtered 2 h after feeding. Reticulo-rumen tissue mass and ruminal epithelium mass in the ventral sac of the rumen were not affected by the MGD. Wet reticulo-ruminal digesta mass decreased from CTRL to MGD7 and then increased, but reticulo-ruminal digesta dry matter mass did not differ between treatments. Omasal mass, omasal tissue mass, and omasum digesta mass decreased linearly with the number of days fed MGD, but abomasal tissue mass tended to increase linearly. Duodenal tissue mass tended to increase linearly, and ileal length increased linearly with the number of days fed MGD. Lactase activity in the proximal jejunum increased linearly and maltase activity in duodenum tended to increase linearly with days fed MGD. Amino-peptidase N activity in the proximal jejunum increased cubically with days fed MGD, and dipeptidylpeptidase IV activity in ileum tended to decrease from CTRL to MGD14 and then tended to increase. Adaptation to a diet with a greater proportion of concentrate involves changes in the mass and length of regions of the gastrointestinal tract and brush border enzyme activity. These changes take place gradually over at least 3 wk.
Key words: starch, adaptation, forestomach, intestine

INTRODUCTION

To increase dietary energy density, diets for high-yielding dairy cows and growing and finishing beef cattle commonly include substantial quantities of grain (Steele et al., 2011; Schwaiger et al., 2013). Although this feeding strategy is necessary to achieve high levels of production, feeding highly fermentable diets poses a challenge for the gastrointestinal tract (**GIT**) epithelium in ruminants (Steele et al., 2011; Liu et al., 2013; Metzler-Zebeli et al., 2013). Consumption of highly fermentable carbohydrates increases the rate of short-chain fatty acid (**SCFA**) production in the rumen, which may lead to SCFA accumulation in the rumen and a reduction in ruminal pH (Aschenbach et al., 2011). Additionally, diets with moderate to high grain content may increase lactic acid production in the rumen and reduce saliva secretion, further reducing ruminal pH (Liu et al., 2013; Chibisa et al., 2016). This situation, commonly referred as subacute rumen acidosis, may lead to less efficient fiber digestion (Calsamiglia et al., 2002; Zebeli et al., 2008), reduced GIT barrier function (Wilson et al., 2012; Liu et al., 2013), translocation of pathogens and endotoxins into the systemic circulation (Plaizier et al., 2008; Li et al., 2012), and liver abscesses (Nagaraja and Titgemeyer, 2007; Plaizier et al., 2008). Furthermore, as the proportion of grain in the diet increases, the amount of starch entering and fermented in the hindgut also increases (Harmon, 2009; Brake et al., 2014). Increased hindgut fermentation can lead to a reduction in large intestinal pH, an increase in endotoxin

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concentration in the digesta, and a corresponding reduction in the expression of tight-cell junction proteins (Li et al., 2012; Metzler-Zebeli et al., 2013).

Cattle should be gradually adapted to diets that are more fermentable (Steele et al., 2011; Schwaiger et al., 2013). Reasons for this include the fact that microbial adaptation and morphological adaptation of the ruminal epithelium require 3 to 9 wk (Dirksen et al., 1985; Tajima et al., 2001; Bannink et al., 2008), and that functional adaptation, although much faster, proceeds over at least 3 wk after a dietary change (Etschmann et al., 2009; Schurmann et al., 2014; Walpole et al., 2015). Although it has been rarely investigated, small and large intestinal tissue mass increases in the first week of lactation, a period associated with an increase in concentrate intake (Reynolds et al., 2004). Therefore, adaptation of the lower regions of the GIT may also require time. However, under practical conditions, cattle often receive substantial increases in rapidly fermentable carbohydrates over a relatively short period. Examples of scenarios in which such rapid dietary change occurs include transition from the dry period to lactation, weaning, arrival at a feedlot, and adaptation to a finishing diet.

The GIT of cattle adapts to an increased proportion of grain in the diet at both morphological and cellular (functional) levels. Increased consumption and the subsequent fermentation of rapidly fermentable carbohydrate results in greater proliferation of ruminal epithelial cells, greater ruminal papillae dimensions, and, in consequence, greater surface area for SCFA absorption (Goodlad, 1981; Bannink et al., 2008; Malhi et al., 2013). The increased surface area of the ruminal epithelium also translates to greater reticulo-ruminal tissue mass (Stobo et al., 1966; Reynolds et al., 2004; Malhi et al., 2013). Furthermore, concentrate intake increases the permeability of ruminal epithelium to SCFA (Amat et al., 2014) by increasing passive and anion exchange pathways for SCFA absorption (Schurmann et al., 2014). Moderate to high grain intake has also been associated with greater abomasal and small intestinal tissue mass (Stobo et al., 1966; Reynolds et al., 2004), indicating a greater importance of those regions of the GIT when the plane of nutrition increases. Additionally, supplementation with concentrate has been reported to increase mRNA expression of sugar transporters in the small intestinal epithelium (Li et al., 2016), and increased provision of concentrate (and its associated greater energy intake) increases brush border enzyme activity (Kreikemeier et al., 1990). On the other hand, lower omasal tissue mass has been observed when the proportion of forage in the diet decreased (Hamada et al., 1976; Bailey, 1986; McLeod and Baldwin, 2000). As a result, adaptation of not only the reticulo-rumen but also the omasum, abomasum, and intestine may be important in determining the efficiency of dietary nutrient use, especially when grain intake is rapidly increased.

An abrupt increase in fermentable carbohydrate intake may have a detrimental effect on ruminal function, because it leads to a reduction in pH, damage of the ruminal epithelium, and less efficient SCFA absorption (Krehbiel et al., 1995; Steele et al., 2011; Schwaiger et al., 2013). At least several days are needed for the ruminal epithelium to recover after bout of ruminal acidosis (Steele et al., 2011; Schwaiger et al., 2013), but less efficient SCFA absorption may be observed for up to the next 3 mo (Krehbiel et al., 1995). This may delay adaptation of the reticulo-rumen (Schwaiger et al., 2013) and other regions of the GIT to dietary change. However, so far, only a limited number of studies have evaluated the time course of changes in the structure and function of the GIT in cattle in response to dietary change (Reynolds et al., 2004; Etschmann et al., 2009; Steele et al., 2011). Knowledge of how the GIT adapts to increased dietary fermentability may increase our knowledge of factors that limit the efficiency of nutrient use in intensively fed cattle.

We hypothesized that the tissue mass of the reticulorumen, abomasum, and small intestine, small intestinal length, and brush border enzyme activity would increase and omasal tissue mass would decrease in response to an abrupt exposure to a diet containing a higher proportion of grain. We further hypothesized that those changes would progress gradually over at least 21 d. The aim of this study was to determine the time course for adaptation of the reticulo-ruminal, omasal, and abomasal tissue mass, small intestinal mass and length, and intestinal brush border enzyme activity in response to an abrupt increase in the proportion of grain in the diet. We also investigated the time course of adaptation for the reticulo-ruminal, omasal, and abomasal digesta mass.

MATERIALS AND METHODS

The steers used for this study were cared for in accordance with the Canadian Council for Animal Care guidelines, and all experimental procedures were preapproved by the University of Saskatchewan Animal Research Ethics Board (protocol 20100021).

Steers and Experimental Diets

Steers used for this study and the experimental procedures have been described elsewhere (Plaizier et al., 2014; Schurmann et al., 2014; Walpole et al., 2015). Briefly, 25 Holstein steers (213 ± 23 kg; 5 to 7 mo of age) fed a common high-forage diet (92% grass hay,