

Sugars in Dairy Cattle Rations

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Abstract

Sugars found in animal feeds include the monosaccharides glucose and fructose and the disaccharides sucrose and lactose. They are part of the larger commonly analyzed fractions of water- and 80% ethanol-soluble carbohydrates. Ruminal microbes convert sugars to organic acids, gases, microbial cells, and glycogen. Fermentation of sugars can produce a greater molar percentage of butyrate than is seen with starch. Glycogen is an internal storage polysaccharide with a structure similar to starch that is produced by ruminal bacteria and protozoa; the sugars other than lactose may be more prone to be converted to glycogen than is starch. Production of glycogen slows the fermentation rate of sugars, potentially helping to maintain higher ruminal pH. Glycogen production can also reduce energy available for microbial growth, but this may be counterbalanced by the rapid rate of microbial growth on some sugars. When substituted for starch or starchy feeds, increasing the amounts of sugars in diets for lactating cows have had varied effects -- not affecting (most studies), increasing, or decreasing milk and milk protein production. A more common effect of sugars is to increase milk fat production. This may be related to production of butyrate or the role of glucose-utilizing microbes in the biohydrogenation of fatty acids. In order to more reliably predict animal performance as we

modify sugar content of rations, we need a better understanding of how the impact of sugars on nutrient supply and rumen function are affected by the levels of sugars fed and other feeds and components in the rations.

Introduction

“Sugars” include the monosaccharides or simple sugars glucose and fructose, and the disaccharides sucrose and lactose (Figure 1). These water-soluble, readily available carbohydrates have digestion characteristics that differ from the starch and fiber carbohydrates in the diet, particularly in how they behave in the rumen. Understanding how ruminal microbes and the cow utilize sugars can help us to understand the basis for the effects we see on animal performance.

Sources and Measurement

There is sufficient variation in the sugar contents of feeds that they can be used to modify the sugar content of diets. Glucose, fructose, and sucrose are found in fresh forage and hays and are affected by stage of maturity and growing conditions of the crop and preservation conditions (2 to 6% of DM in legumes and warm season grasses, up to 8 to 15% in some cool season grasses; Smith, 1973). Silages tend to have little residual sugar after fermentation, but this can increase to a few percent in well preserved

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forages with higher DM concentrations (M.B. Hall, unpublished), or up to 40% (measured as nonstructural carbohydrate) in high sugar silages such as that made with sugar cane (Sousa et al., 2014). Fruit and vegetable pulps, such as citrus and beet pulps, can contain substantial amounts of sugars that vary with the amount of citrus or beet molasses applied (citrus pulp: 12 to 40% as ethanol-soluble carbohydrates; Hall, 2001). Cane or beet molasses vary in sugar content depending upon the blends of ingredients present in the final product. Almond hulls (20 to 29%; Aguilar et al., 1984), and even soybean meal (6 to 7%; Choct et al., 2010) can contribute sugars to the diet. Lactose is found only in milk products, such as whey (70%; Defrain et al., 2004) and whey permeate (76 to 85%; American Dairy Products Institute, 2016).

Commonly used feed analyses do not measure sugars alone, but include them in larger fractions. Water-soluble carbohydrates (**WSC**) and 80% ethanol-soluble carbohydrates (**ESC**) include sugars but also contain other carbohydrates. The WSC include simple sugars, both sucrose and lactose, short chain carbohydrates (oligosaccharides), and possibly some of the polysaccharides, such as long and short chain fructans. The ESC contains the same carbohydrates as WSC except that it does not fully solubilize lactose (Machado et al., 2000) or long chain polysaccharides (Asp, 1993), including the long chain fructans. Based on our present understanding, the ruminal fates of the WSC are sufficiently similar, except for rates of fermentation, to keep them as a group.... but don't call them "sugars".

An assay used on molasses that does measure sugar content is "total sugars as invert". This analysis provides a value for the sum of sucrose, glucose, and fructose in molasses. If whey was added to the molasses to help it flow, the value may or may not include lactose, or

may count only half of the lactose, depending on the analysis used.

Utilization of Sugars in The Gut

Cattle themselves have the capacity to digest starch, lactose, and the microbial storage carbohydrates glycogen and the disaccharide trehalose, based on enzymes present in the pancreatic secretions and the membrane lining the small intestine (Kreikemeier et al., 1990). All other carbohydrates, including sucrose, fructans, pectins and those in neutral detergent fiber, must be degraded and utilized by ruminal or other gastrointestinal microbes for them to provide nutrients to the animal. Based on their solubility, sugars likely flow with liquid in the gut.

Microbial products

Sugars disappear very rapidly from the rumen, with rates of glucose disappearance of 422 to 738% per hour (Weisbjerg et al., 1998). Microbial fermentation of sugars is generally reported to give greater molar percentages of butyrate and lactate than does starch (Strobel and Russell, 1986; DeFrain et al., 2004; Hall et al., 2010). But the yield of microbial nitrogen from sugars like sucrose has been reported to be lower than from starch (Hall and Herejk, 2001; Sannes et al., 2002). However, organic acid and microbial cell growth do not tell the whole story.

We've traditionally thought of ruminal disappearance of carbohydrates in terms of microbes converting them into organic acids (lactate, acetate, propionate, butyrate, valerate), gases (carbon dioxide and methane), and microbial cells, or having the carbohydrates pass undegraded through the rumen. But, there are other products that ruminal microbes can make in appreciable quantities, and one of them is glycogen (Figure 2). Glycogen is a

polysaccharide with a structure very similar to starch. It is made and stored internally by both protozoa and bacteria and may be fermented by the host microbe. Glycogen may pass from the rumen with the passage of microbes, such that there can be a significant flow of glycogen (with potential to digest like starch) to the small intestine, even on all forage rations (Branco et al., 1999). Glycogen production essentially slows down fermentation and acid production, relative to the rate of the readily available carbohydrate from which it was formed. But, a hidden cost of glycogen production is that it costs 1 ATP to add a glucose to the glycogen chain (Ball and Morell, 2003). To put this in perspective, if rumen microbes obtain 3 to 4 ATP from fermenting a carbohydrate (Russell and Wallace, 1988), transiently storing glucose as glycogen effectively decreases the ATP yield by 25 to 33%, reducing the amount of energy available to drive microbial cell production. The facts that not all of the carbohydrate that microbes took up has yet been fermented to energy that drives microbial cell growth, and that the available ATP has been reduced may be the basis for reported reductions in microbial nitrogen production with sugars as compared to starch (Hall and Herejk, 2001; Sannes et al., 2002).

Sugars may be more prone to be converted to glycogen than many other carbohydrates because of how rapidly available they are in the rumen. More microbial glycogen is made when greater amounts of rapidly available carbohydrate are present (Prins and Van Hoven, 1977), particularly if there is more available relative to the microbes' need for energy (Ball and Morell, 2003). In this light, glycogen this may be an alternative strategy to energy spilling where microbes produce ATP from fermenting carbohydrate, but then waste the energy as heat. Increased availability of ruminally degradable protein (**RDP**) can decrease glycogen production

(McAllan and Smith, 1974) and increase the flux of carbohydrate through fermentation, which can also increase ruminal lactate production (Counotte and Prins, 1981; Malestein et al., 1984). Given glucose as a substrate, ruminal microbes prefer to use amino nitrogen (amino acids, peptides) rather than ammonia or urea (Hristov et al. 2005) and may produce more microbial protein with peptides than urea (Figure 3; Hall, 2017).

Effects of sugars on ruminal fiber digestion have varied among studies. Supplementation of cattle diets with feeds high in sugar have depressed fiber digestion, even when ruminal pH is not greatly reduced (Pate, 1983). Sugar supplements can depress fiber digestion through effects of pH (Khalili and Huhtanen, 1991), inhibitors produced by the microbes (Piwonka and Firkins, 1996), and if RDP is limiting (Heldt et al., 1999). In the latter case, it may be a matter of the sugar-utilizers outcompeting fiber-users for scarce nutrients (Jones et al., 1998). However, sugars may not be all bad: there is some evidence that they may increase fiber digestion if protein is not limiting (Heldt et al., 1999) (Figure 4).

Sugar-utilizing microbes also have a role in the biohydrogenation of fatty acids in the rumen which may affect milk fat production. Some species of glucose-utilizing microbes perform biohydrogenation on fatty acids in the rumen (e.g., *Butyrivibrio fibrosolvens*; McKain et al., 2010). The trans-10 isomer of the 18:1 fatty acid has been implicated in milk fat depression. When sucrose was supplemented as 4.7% of ration DM, the concentration in the milk of total trans 18:1 fatty acids declined and milk yield had a tendency to increase (Penner and Oba, 2009). In one study, addition of 2.6% molasses blend product that added 1.5% invert sugars to the diet was associated with an increase in the trans-10 18:1 concentration in milk, but it

was questioned as to whether this was a molasses product effect, or related to urea feeding on some diets containing the molasses product (Oelker et al., 2008).

Another difference between sugars and other carbohydrates like starch is strictly a matter of how much sugar is actually there in terms of hexoses, or single 6-carbon sugars. Glucose, fructose, and galactose are hexoses. One glucose = 1 hexose that is not bound to another sugar, so 1 lb of glucose = 1 lb of free hexose. Sucrose or lactose contain 2 hexoses that are bound to each other. To put them on the same free hexose basis as glucose, the molecules have to be hydrolyzed to release the free sugars, which means you have to add the weight of water used to hydrolyze them, which nets 1.05 lb free hexose per pound of disaccharide. In polysaccharides like starch, there are many bonds that need to be hydrolyzed by the addition of water, and so 1 lb of starch = 1.11 lb of free hexose. So, the same DM weight of starch has more total free hexose than sugars. Does this matter? If the microbes can use sugars more efficiently than starch because they can ferment them more rapidly (think dilution of maintenance), then maybe not, but it is another piece that can factor into the value of carbohydrates to the microbes or cow.

Lactose different than other sugars?

The way microbes handle lactose seems to be different from other sugars, possibly because of its slower rate of utilization. In fermentations using ruminal inoculum from cows that had been fed glucose and lactose for 2 weeks so that the microbes were adapted to using the sugars, there was slower carbohydrate disappearance and organic acid production with lactose than with glucose (Figure 5; Hall, 2016). There was much more glycogen production with glucose, though lactose fermentations produced enough to maintain the initial level of glycogen.

Microbial nitrogen yield was lower with lactose. Lower microbial nitrogen and glycogen production for lactose may have been related to its much slower rate of use by the microbes.

Animal Performance

Based on microbial use of sugars, how might sugars affect animal performance? The results we see in research studies are affected by how much and what type of sugar was included, what the background level of WSC was in the diet, and what the other ration ingredients were. At this point, we do not have sufficient information to state exactly how sugars will affect performance under different circumstances. However, with an understanding of how sugars are processed in the gut, we may hazard some ideas on what factors can affect cow performance.

Milk production

In research studies, supplementation with sugars or sugar sources did not affect milk production when substituted for starch or starch sources (Nombekela and Murphy, 1995; McCormick et al., 2001; Sannes et al., 2002; DeFrain et al., 2004; Broderick et al., 2008; Oelker et al., 2008; Hall et al., 2010), or increased production to a point then declined above 5 to 6% total sugars as ESC in the diet (Broderick and Radloff, 2004), or depressed milk production in late lactation cows (Oelker et al., 2008). A key element here may be simply making sure that enough digestible carbohydrate is provided to the animal to meet energy needs.

Milk fat

Sugars have been reported to increase milk fat production (lb/day; Nombekela and Murphy, 1995; Broderick and Radloff, 2004; Broderick et al., 2008; Penner and Oba, 2009),

but that response is not always seen (McCormick et al., 2001; Cherney et al., 2003; DeFrain et al., 2004; Oelker et al., 2008). Milk fat production was depressed when sucrose addition in late lactation cows also depressed milk production (Sannes et al., 2002). One way that sugars could have a positive impact on milk fat is through biohydrogenation of fatty acids to reduce availability of those that can cause milk fat depression. That would require that unsaturated fatty acids that could become a problem are present in the diet in sufficient amounts to potentially be an issue. It could also require that the rate of liquid passage is at a rate that allows the microbes and fatty acids to remain in the rumen long enough for biohydrogenation to occur. Another potential option to affect milk fat is through production of butyrate. Ruminal infusions of butyrate or acetate were shown to increase the milk fat percentage and not depress milk yield, but milk production of animals on the studies were quite low (Rook and Balch, 1961; Rook et al., 1965). Although butyrate makes up a small proportion of the fatty acids in milk, it constitutes approximately 30% of the fatty acids in the sn-3 position in milk triglycerides (Jensen, 2002) and can be used to make other short chain fatty acids that are secreted in milk.

Milk protein

Milk protein production (lb/day) has been reported to increase and then decrease with increasing sugar addition (maximum response at ~added 3 to 6% sugars then declined; Broderick and Radloff, 2004), be unaffected by sugar addition as a substitution for starchy feeds (Nombekela and Murphy, 1995; McCormick et al., 2001; Cherney et al., 2003; DeFrain et al., 2004; Broderick et al., 2008; Oelker et al., 2008), decrease with sucrose addition (Sannes et al., 2002; milk production depressed), or be equivalent to starch when more undegradable protein was increased in the diet or less than

starch with more dietary RDP (Hall et al., 2010). The effect of sugar inclusion will likely be a matter of how rapidly the microbes are grown and the degree to which they pass from the rumen to where the cow can digest them, and whether the amino acids that the microbes provide are a limiting nutrient for milk protein production. We may be able to get more microbial protein produced from sugars if we provide true protein / peptides rather than urea. That could also result in less glycogen production and the associated reduction in energy available for microbial growth. Another thing to consider is shown in Figure 5. Compared to slowly used lactose, even though the microbes made much more glycogen when given glucose, they still made more microbial protein. That could be a function of dilution of maintenance – even with the glycogen drain on ATP, the microbes were using the glucose so quickly that the amount of the energy that they spent on maintenance was a smaller proportion than they spent on growth; just like the feed efficiency of energy spent on milk production vs. maintenance for a high producing cow vs. a low producer. Delivery of protein from sugar-utilizing microbes to the cow may also have the advantage that those microbes have potential to pass from the rumen more quickly as they move with the liquid, rather than the much slower passage with the solids.

Ruminal pH

Generally, sugars have not had the negative impact on ruminal pH that one might expect from a potentially rapidly fermenting carbohydrate that can ferment to lactic acid. When comparing sugars or sugar sources vs. starch or starch sources in lactating dairy cows, ruminal pH was unaffected (McCormick et al., 2001; Sannes et al., 2002; Broderick and Radloff, 2004; DeFrain et al., 2004; Broderick et al., 2008; Oelker et al., 2008) or increased (Penner and Oba, 2009) as sugars in the

diets were increased. Lactating cows given a molasses + sucrose-containing diet with more undegradable protein had a similar rumen pH to diets containing ground corn or citrus pulp as the main nonfiber carbohydrate source (average pH in 6 hours after feeding = 6.0). But, a molasses + sucrose diet with more RDP had an average ruminal pH of 5.7 in the same time frame (Hall et al., 2010). When beef steers were fed low-quality tallgrass-prairie hay supplemented with 0.122% of BW as supplemental RDP and 0.30% of BW as glucose, fructose, or sucrose, ruminal pH reached its lowest point at 3 hours post-feeding, the earliest sampling point for the sugars; whereas, ruminal pH of cattle receiving starch reached the lowest point at 9 hours post-feeding (Heldt et al., 1999); the average ruminal pH of the starch-fed animals was lower than those receiving one of the sugar treatments which did not differ. A study on induced ruminal acidosis showed that ruminal pH declined more rapidly with the molasses treatment, but also began to recover after 24 hours, whereas the pH declined for 120 hours in animals given crushed wheat (Randhawa et al., 1982). This could be related to molasses and microbes flowing from the rumen with the liquid fraction, whereas wheat grain might be more likely to remain in the rumen with the solid fraction. How could a potentially rapidly fermented carbohydrate like sugars be having these effects? Slowing fermentation through production of glycogen or passage with the liquid fraction may temper the impact of sugar on ruminal pH. Increasing RDP may decrease glycogen production and increase the rate of fermentation and impact on ruminal pH – is RDP a governor for the effect of carbohydrates on pH? So, paying attention to the overall rate of fermentation/availability of the sugars and starch portions of the diet may dictate modifying the amounts of RDP that is fed to maintain a healthy rumen and supply nutrients to the cow.

How much sugar can we feed?

This is an open question because the work has not been done to test it adequately with high producing cows on the variety of rations that are fed commercially. And, we need to remember that including FEEDS that contain sugars may have different results than feeding sugars by themselves because there are other fractions in real feeds that could affect results. The highest levels of “sugars” as sugar proper or as ESC that have been fed to cows on research studies are 7.5% sucrose / 10% ESC (Broderick et al., 2008), 12% ESC from sucrose, molasses, and citrus pulp (Hall et al., 2010), and 13% lactose (DeFrain et al., 2004). In these studies, the main substitutions were sugar sources for starch sources. The most extreme feeding approach was 21% of diet DM as nonstructural carbohydrates from freshly cut sugarcane fed in addition to a concentrate mix to growing Nellore steers (Sousa et al., 2014). The 18 month old 606 lb steers consumed 10 to 13 lb of the total diet and had ruminal pH of 6.4 to 6.7.

Conclusions

Research on sugars substituted for starch have shown a variety of effects on ruminal microbe and animal performance. Increases in milk fat production and unchanged or increased ruminal pH are more common results that are in line with our understanding of how ruminal microbes process sugars, but the responses are not always seen. In order to know how best to incorporate sugars into diets for lactating dairy cows to reliably get the desired results, we need to understand what variables may be altering the picture. As we modify sugar content of rations, we need a better understanding of how the impact of these carbohydrates on nutrient supply and rumen function are affected by the levels of sugars fed and the other feeds and components in the rations, perhaps particularly including ruminally degradable protein and fatty acids.

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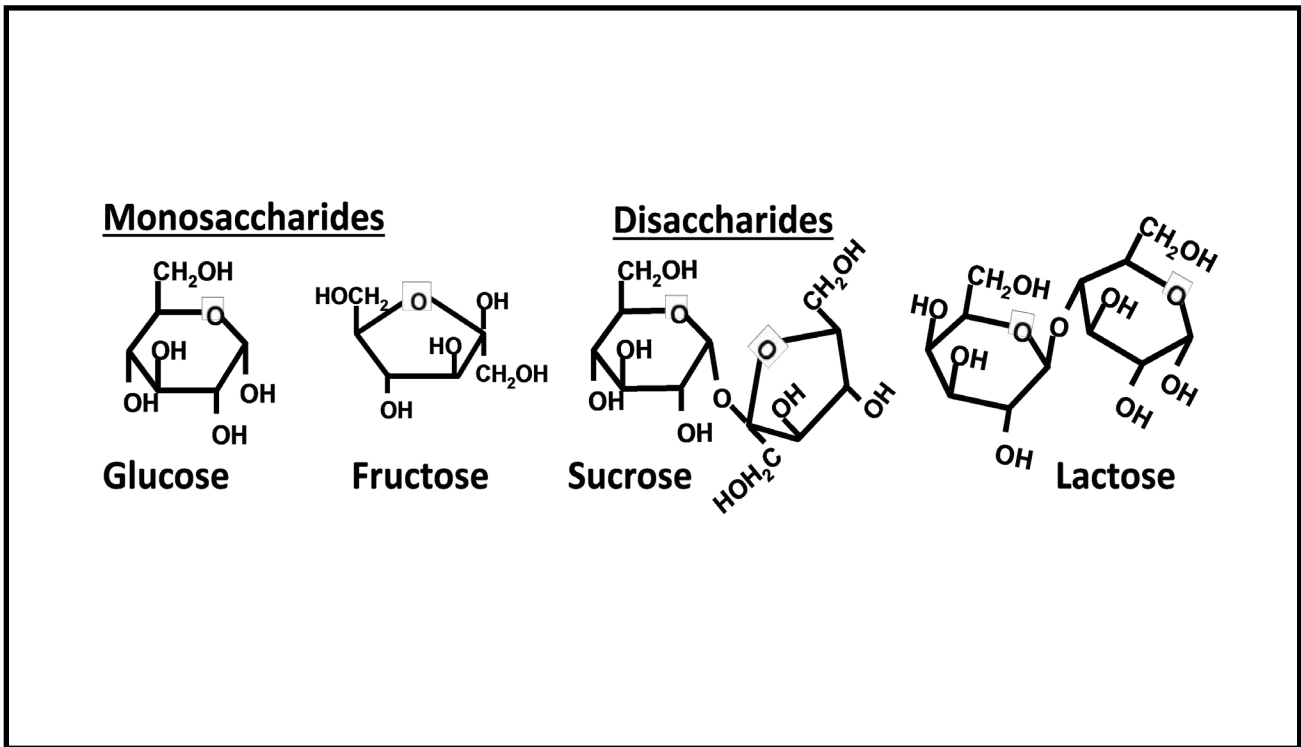


Figure 1. Chemical structure of sugars. Sucrose = glucose + fructose, Lactose = glucose + galactose.

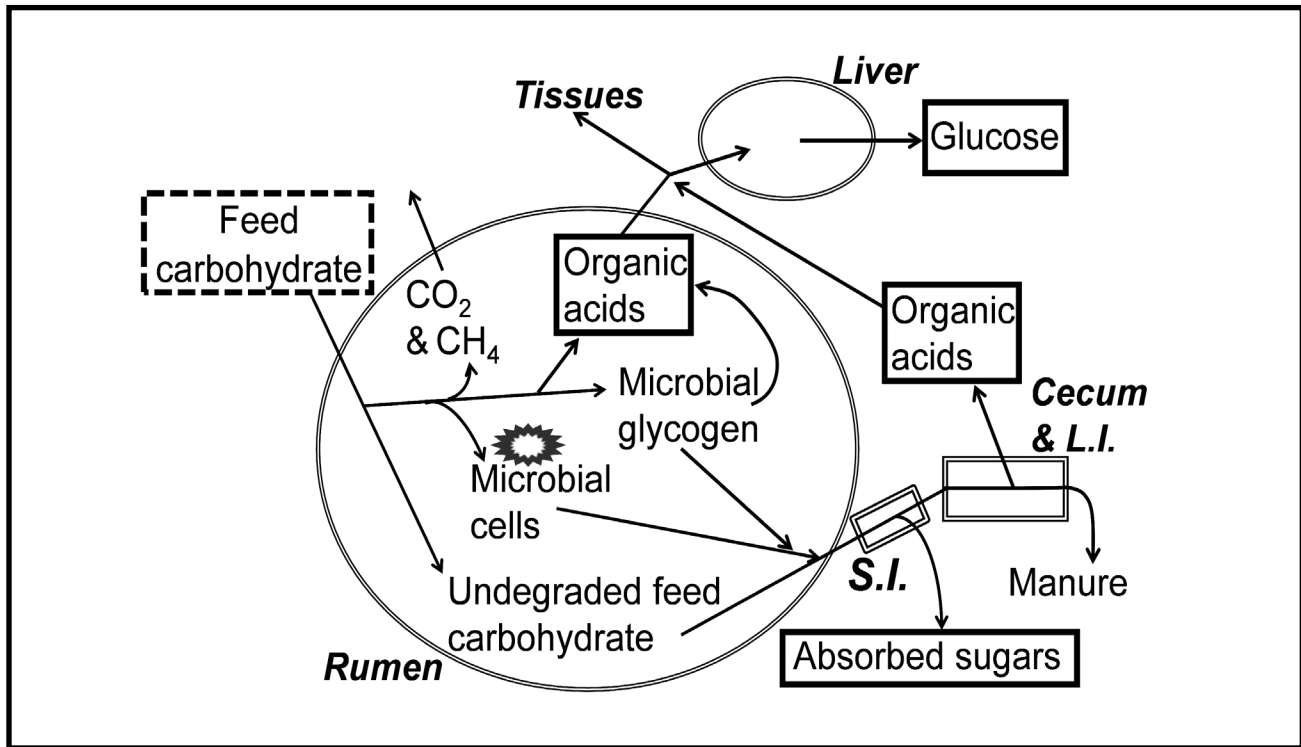


Figure 2. Fates of carbohydrates. SI = small intestine, LI = large intestine.

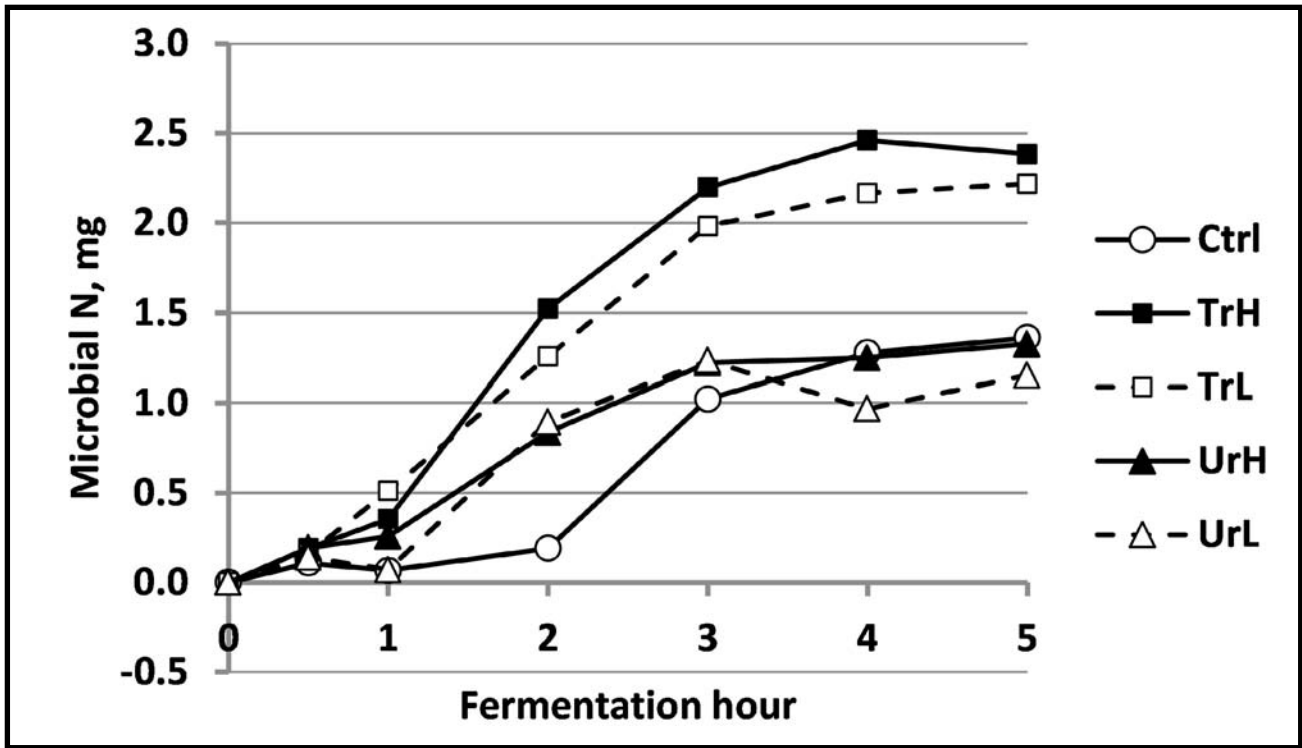


Figure 3. Responses in microbial nitrogen (N) production with glucose as a substrate and different concentrations of N, peptides (Tr) and urea (Ur) in the fermentation media. Ctrl = lowest N, L = Increased low level of N, and H = Increased highest level of N. (Hall, 2017).

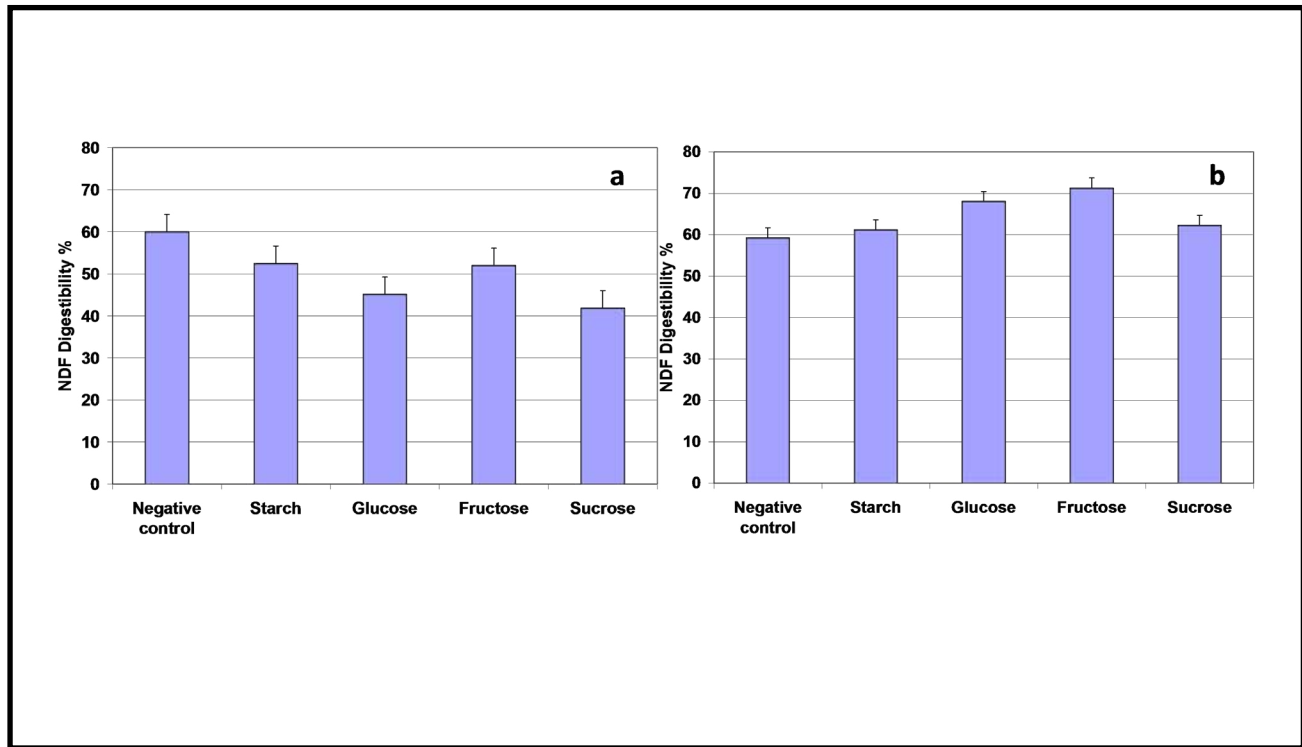


Figure 4. Total tract digestibility of NDF with different nonfiber carbohydrates and ruminally degradable protein (RDP) supplementation. Graph a: RDP supplemented at the lower level of 0.031% of body weight; Graph b: RDP supplemented at the higher level of 0.122% of body weight (Heldt et al., 1999).

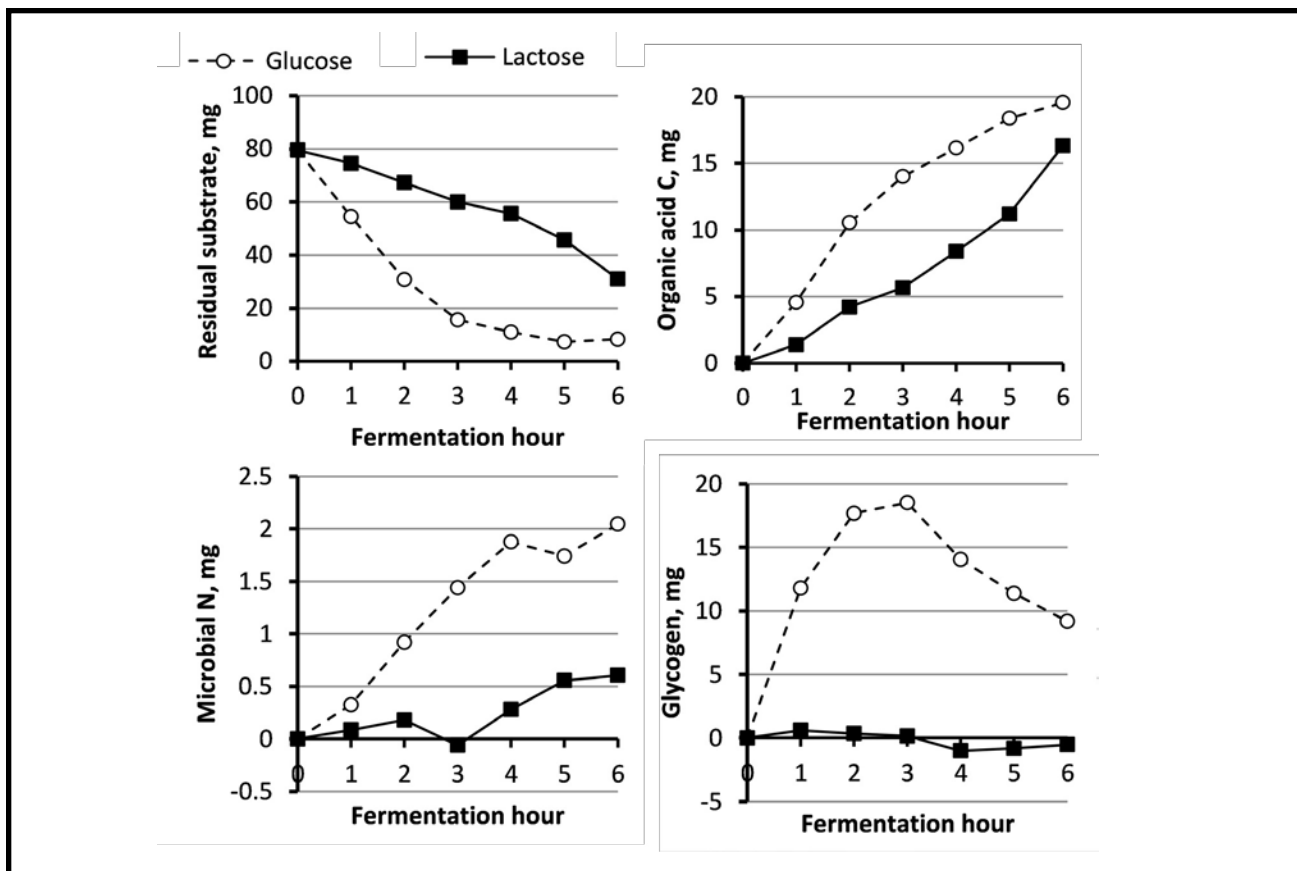


Figure 5. Use of glucose and lactose by mixed ruminal microbes in vitro (treatments with 300 mg nitrogen / L fermentation medium, including both ammonia and peptides; Hall, 2016).