Bioactive Carbohydrates and Dietary Fibre xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Bioactive Carbohydrates and Dietary Fibre

journal homepage: www.elsevier.com/locate/bcdf

Impact of resistant vs. digested starch on starch energy value in the pig gut

Janelle M. Fouhse, Ruurd T. Zijlstra*

Department of Agricultural, Food and Nutritional Science, University of Alberta, 4–10 Agriculture/Forestry Centre, Edmonton, AB, Canada T6G 2P5

ARTICLE INFO

Keywords:
Digestion
Energy
Fermentation
Starch

ABSTRACT

A major energy substrate for monogastric species such as humans and swine is starch from cereal grains, pulses and tubers. The rate, site and extent of starch digestion in the gastro-intestinal tract are dependent on the intrinsic factors of starch origin and the extrinsic factors such as applied processing methods. In monogastric species, starch escaping small intestinal digestion becomes readily available for microbial fermentation in the hindgut and has been coined resistant starch (RS) accordingly. Host physiological and metabolic responses differ according to the site and rate of starch digestion; however, the quantity of energy derived to the host from fermented vs. digested starch remains debated. A detailed understanding of the underlying mechanisms that cause nutrient flow and substrate availability in the hindgut to alter host energy metabolism and growth potential is lacking. Dietary RS may in fact have nearly equal energetic efficiency as digested starch due adequate provision of short chain fatty acids (SCFAs) and decreased energy loss due to decreased activity. Thus, proper characterization of the energetic efficiency of purified and whole grain starch sources is required for accurate diet formulation. This review will focus on how various methodologies can be used to quantify site, extent and kinetics of starch digestion, illustrating the differences in energetic efficiency between RS vs. digested starch.

1. Introduction

Starch from cereal grains is the main source of energy in swine diets, representing up to 55% of the diet (Knudsen, Lærke, Steenfeldt, Hedemann, & Jørgensen, 2006). The rate of starch digestion into single glucose units varies dependent on the chemical composition and processing methods applied to starch (Giuberti, Gallo, Moschini, & Masoero, 2015). Starch escaping small intestinal digestion, i.e., resistant starch (RS), becomes a substrate for microbial fermentation resulting in production of short chain fatty acids (SCFA). The microbial products of RS fermentation SCFA are preferential energy substrates for the gut. Consequently, consumption of RS can bolster gut health through promotion of important physiological functions in the gut such as epithelial barrier function, cell proliferation and pathogen exclusion, as has been reviewed previously (Bird & Hayakawa, 2000; Bird, Brown et al., 2000; Keenan et al., 2015). In swine nutrition, whether dietary RS vs. digested starch reduces growth and efficiency due to differences in energetic efficiency of utilization is debated. Rapidly digested starch is thought to be at least 14% more efficient at yielding energy vs. RS that is fermented into SCFA (Jørgensen, Larsen, Zhao, & Eggum, 1997). As such, starch varying in rate and site of digestion will influence its energy value and host physiological responses including feed intake, growth, lean and fat deposition, hormonal homeostasis, microbial ecology and gut health. Thus, proper evaluation of the energy value of starch, especially resistant starch (RS), is needed for accurate diet formulation.

In North American, predictive net energy (NE) equations adapted from (Noblet, Fortune, Shi, & Dubois, 1994) are conventionally used (NRC, 2012). These predictive equations calculate NE based on measured DE or ME value of ingredients, for example: NE = (0.700 × DE) + (1.61 × ether extract) + (0.48 × starch) – (0.91 × crude protein) – (0.87 × acid-detergent fibre). These prediction equations have limitations, e.g., the NE value of high fibrous ingredients will be overestimated. Because these equations use total starch content they may also overestimate energy content in high RS ingredients. However, if these prediction equations indeed overestimate energy content of RS-containing ingredients, the proper measurement to determine digestibility and energy value of starch remains a question.

Classical swine nutritionists have measured starch digestibility as apparent total tract digestibility (ATTD). However, this method does not differentiate between starch digestion and fermentation and typically results in 100% digestibility (Cervantes-Pahm, Liu, & Stein, 2014; Sun, Lærke, Jørgensen, & Knudsen, 2006). To distinguish site, extent and kinetics of starch digestion is of nutritional interest; thus, methodologies have been designed and include: use of simple cannulas (Low, 1980), slaughter (Payne, Combs, Kifer, & Snyder, 1968), installation of catheters to measure glycemic index (GI) and starch-derived portal vein nutrient fluxes (Rerat, Vaissade, & Vaugelade, 1984a, 1984b), *in vitro*

* Corresponding author.
E-mail address: ruurd.zijlstra@ualberta.ca (R.T. Zijlstra).

http://dx.doi.org/10.1016/j.bcdf.2017.08.001
Received 28 August 2016; Received in revised form 15 July 2017; Accepted 3 August 2017

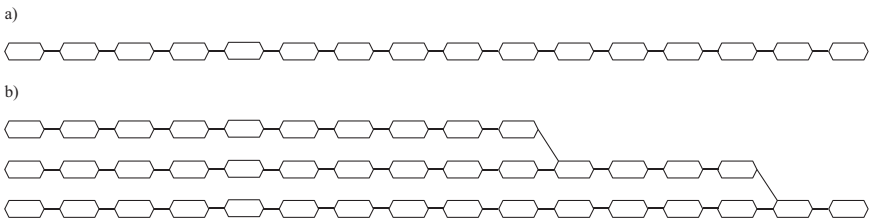

Fig. 1. Schematic of a) amylose and b) amylopectin showing their linear and branched structure, respectively.

assays mimicking small intestinal digestion (Englyst, Kingman, & Cummings, 1992) and indirect calorimetry to measure energy value. This review will focus on methodologies used to quantify site, extent and kinetics of digestion of RS vs. digested starch in pigs. How these techniques can illustrate differences in digestibility between RS vs. digested starch and consequently energetic efficiency and animal growth will be emphasized.

2. Factors influencing rates of starch digestion

2.1. Chemical composition

Starch is comprised of amylose and amylopectin, making up 98–99% of dry weight, with the remaining 1–2% being integral lipids in the form of lysophospholipids or free fatty acids (Tester, Karkalas, & Qi, 2004). Both amylose and amylopectin are polymers of glucose consisting of α – 1,4 linkages and α – 1,6 branches in the case of amylopectin (Fig. 1) (Annison & Topping, 1994; Ao et al., 2007). Classically, starch can be considered waxy, normal or high amylose with < 15%, 20–35% and > 40% amylose content, respectively (Tester et al., 2004). Amylopectin has an increased rate of digestion, due to digestive enzymes reaching multiple reducing ends (Copeland, Blazek, Salman, & Tang, 2009). Amylose tends to form insoluble semi-crystalline aggregates during processing and is less digestible (Copeland et al., 2009).

The components of starch amylose and amylopectin are packaged into alternating crystalline and amorphous regions in granules. The amylose and amylopectin containing granules come in a variety of sizes and shapes, dependent on ingredient source and arrangement of amylose and amylopectin within the crystalline regions (Copeland et al., 2009; Lindeboom, Chang, & Tyler, 2004). Small granules have a greater digestibility than large granules due to increased surface area (Bednar et al., 2001; Manelius & Bertoft, 1996; Vasanthan & Bhatty, 1996).

Naturally occurring proteins, lipids and fibrous components of cereal grains interact within a cereal grain matrix to impact rate and efficiency of starch metabolism with the matrix components slowing gastric emptying and digestion (Thompson, Yoon, & Jenkins, 1984). Lipids–amylose complexes can increase the hydrophobicity of starch granules, impeding digestibility (Vasanthan & Bhatty, 1996). Protein–amylose complexes within the cereal grain matrix also reduce the SI digestion rate of the ingredient and subsequent GI (Jenkins, Thorne, Wolever, Rao, & Thompson, 1987). Other components including lectins, tannins and phytic acid may inhibit enzymatic degradation in the SI further slowing down glucose absorption (Jenkins et al., 1987; Thompson et al., 1984). Lowered glycemic response is correlated with the presence of phytic acid, an anti-nutritional factor, which is explained by a decrease in the rate of digestion (Yoon, Thompson, & Jenkins, 1983).

To increase digestibility and feed acceptance of grains to pigs, raw grains are typically processed such technologies such as cracking, grinding, rolling, flaking pelleting, steaming, expanding and extruding. In particular application of heat - processing on starch-containing ingredients disrupts the crystalline regions and increase α-amylase susceptibility and bioavailability (Bornet, 1993). How starch structure and processing affects digestibility has been described previously (Giuberti et al., 2015).

3. Starch metabolism

3.1. Digestion

The nutritive value of starch-containing ingredients is associated with composition and rate, site and extent of digestion. As previously reviewed, digestibility of starch-containing ingredients is dependent on intrinsic and extrinsic factors including botanical origin and processing methods. Starch hydrolysis begins with an endo-hydrolyase, salivary α–amylase; however, action of this enzyme is short lived due to timely passage of feed to the stomach. Once in the stomach, HCl secretion by parietal cells increases acid hydrolysis of starch at the expense of salivary α–amylase activity. Although salivary α–amylase plays only a minor role in starch hydrolysis, it is hypothesized to be part of a chemosensing mechanism, aiding in the maintenance of hormonal homeostasis (Shirazi-Beechey, Moran, Batchelor, Daly, & Al-Rammahi, 2011).

Once in the SI, pancreatic secretions into the duodenum increase pH and restart enzymatic starch hydrolysis with porcine pancreatic α–amylase (PPA). Starch hydrolysis by α–amylase can be rate limited due to the intrinsic properties of starch (Slaughter, Ellis, & Butterworth, 2001). The PPA works in a multiple attack mechanism forming a stable substrate-enzyme complex enabling hydrolysis of multiple bonds (Robyt & French, 1967). The PPA has both endo and exo–hydrolysis action, first hydrolysing the α–1,4 linkages and subsequently hydrolysing the newly formed reducing end (Koukiekolo, Desseaux, Moreau, Marchis-Mouren, & Santimone, 2001; Robyt & French, 1970). The exo–hydrolysis action of PPA produces short malto–oligosaccharides and α–limit dextrins (MacGregor, Janeček, & Svensson, 2001). Limited studies have assessed action of PPA on amylopectin, even though amylopectin forms the majority of most native starches. The PPA has a low inner chain attack activity on amylopectin, resulting in slower hydrolysis rate (Bijttebier, Goesaert, & Delcour, 2010). The finding that PPA hydrolysis of amylopectin might be slower than amylose has caused a new theory to emerge that branching density of amylopectin and amylose may be a factor influencing starches digestibility (Ao et al., 2007).

Mucosal enzymes digest α–limit dextrins left by amylase hydrolysis. Four mucosal enzymes exist, including N terminus and C terminus subunits of maltoglucoamylase and sucroisomaltase that convert limit dextrins to free glucose. More sucroisomaltase than maltoglucoamylase exist in the SI; however, the order of digestion capacity is C terminus maltoglucoamylase, C terminus sucroisomaltase, N terminus sucroisomaltase, N terminus maltoglucoamylase. Recently-detected, mucosal enzymes may be important to determine starch digestion rate. For example, certain α–limit dextrins were resistant to digestion by α–glucosidases (Lin et al., 2012).

3.2. Fermentation

The portion of starch resisting host enzymatic digestion, termed RS in 1982 by Englyst, flows to the distal ileum, caecum and large intestine becoming an ideal substrate for microbial fermentation. Fractions of starch resistant to digestion have been divided into 5 subtypes based on physical and chemical characteristics and are reviewed in detail elsewhere. For the purpose of this review, RS will refer to RS1, physically