Animal Nutrition 4 (2018) 305–310

Contents lists available at ScienceDirect

Animal Nutrition

journal homepage: http://www.keaipublishing.com/en/journals/aninu/

Review Article

Application of resistant starch in swine and poultry diets with particular reference to gut health and function

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ARTICLE INFO

Article history:
Received 16 August 2017
Received in revised form 27 February 2018
Accepted 2 April 2018
Available online 13 April 2018

Keywords:
Resistant starch
Swine
Poultry
Gut health and function
Growth performance

ABSTRACT

The immediate post-weaning period poses a major challenge on the survival of piglets. Similarly, newly hatched chicks face life threatening challenges due to enteric infections. In the past several years, in-feed antibiotics have been used to reduce these production problems and improve growth. However, in-feed antibiotics have been banned in many jurisdictions and therefore the most effective alternatives to in-feed antibiotics must be developed. To date, several studies have been conducted to develop alternatives to antibiotics. One of the potential candidates as alternatives to in-feed antibiotics is resistant starch (RS). Resistance starch is a type of starch that resists enzymatic digestion in the upper parts of the gastrointestinal tract and therefore passes to hindgut where it can be fermented by resident microorganisms. Microbial fermentation of RS in the hindgut results in the production of short chain fatty acids (SCFA). Production of SCFA in turn results in growth and proliferation of colonic and cecal cells, increased expression of genes involved in gut development, and creation of an acidic environment. The acidic environment suppresses the growth of pathogenic microorganisms while selectively promoting the growth of beneficial microbes. Thus, RS has the potential to improve gut health and function by modifying and stabilising gut microbial community and by improving the immunological status of the host. In this review, we discussed the roles of RS in modifying and stabilising gut microbiota, gut health and function, carcass quality, and energy metabolism and growth performance in pigs and poultry.

1. Introduction

The immediate post-weaning period poses major challenges in the nutritional management of piglets and has direct consequences on their growth performance from nursery to market weight. Similarly, newly hatched chicks face life threatening enteric infection. These periods are characterized by poor feed intake (FI), which is in concert with the immature digestive and immune system that predisposes piglets and baby chicks to various diseases such as diarrhoea (Pluske et al., 1998).

About 20 years ago, the use of in-feed antibiotics and some other antimicrobial compounds that have been used as performance enhancers became the target of increasing public criticism and political controversy (Vondruskova et al., 2010). Thus, in the past 2 decades, an extensive amount of research has been conducted to develop alternatives to in-feed antibiotics to maintain animal health and performance (Shim et al., 2005; Zimmermann et al., 2001; Erickson and Hubbard, 2000). One of the alternatives to in-feed antibiotics is the use of feed additives such as resistant starch (RS) which are known to confer prebiotic effects. Resistant starch is a constituent of dietary fiber that cannot be broken down by the host's digestive enzymes in the small intestine but can be fermented by microorganisms in the lower gastrointestinal tract (Landon and Salman, 2012). Hence, RS does not release monosaccharide within the small intestine. However, it is fermented to a large extent by microbiota in the colon, resulting in the production of short-chain fatty acids (SCFA) (Topping and Clifton, 2001; Bird et al., 2007).

There are 4 different types of RS (Sajilata et al., 2006). Resistant starch 1 is a starch that is found in grains and legumes. Resistant

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Peer review under responsibility of Chinese Association of Animal Science and Veterinary Medicine.

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https://doi.org/10.1016/j.aninu.2018.04.001

starch 2 is the one that is found in some starchy foods, including raw potatoes and green (unripe) bananas. Resistant starch 3 is formed when certain starchy foods, including potatoes and rice, are cooked and then cooled. Resistant starch 4 is a starch that is formed via a chemical process.

Diets rich in RS have health and animal welfare benefits, such as lowering postprandial glycemia and insulinemia, enhancing absorption of minerals including calcium and iron, and prolonging the duration of satiety (Sajilata et al., 2006; Da Silva et al., 2012). The fermentation by-products of RS, SCFA also contribute to the health of the host in many ways (Landon and Salman, 2012). The suitability of any feed additive as alternative to in-feed antibiotics should be tested in an experiment where the efficacy of test additive is compared with antibiotics in boosting gut health and function. However, so far very few studies have examined the effect of RS on gut health and function in comparison with in-feed antibiotics (Leeson et al., 2005; M'Sadeq et al., 2015).

Several studies were conducted to examine the effect of different types of RS on gut health and function. Although most of them have been reported to improve gut health and function, results from few studies were inconsistent. This review was conducted to summarise the current state of knowledge on the use of RS to improve gut health and provide practical recommendations to further investigate the suitability of RS as one of the alternatives to in-feed antibiotics.

2. Resistant starch and gut health

2.1. Effects of resistant starch on gut health and growth performance

The immediate post-weaning period is a critical time for the survival of piglets. Newly weaned pigs depend on passive immunity from sows' milk. Piglets do not have access to the passive immunity from mothers' milk after weaning. Piglets are exposed to pathogenic challenges and unfortunately their gastrointestinal barrier function is not well developed at this time. Hence, this period is characterised by post-weaning growth lag causing tremendous economic losses to the swine industry. Additionally, major qualitative and quantitative changes in the gastrointestinal microbiota of pigs take place at this time. Similarly, newly hatched chicks are confronted with stressful situations such as long distance shipping (Chou et al., 2004) and enteric infections by coccidia and avian pathogenic *Escherichia coli* (Kemmett et al., 2014; Olsen et al., 2012), and respiratory diseases that are responsible for growth depression or death (Olsen et al., 2012).

Resistant starch is completely degraded in the cecum leading to changes in cecal and colonic microbiota composition, increases in cecal and colonic SCFA concentrations (Martin et al., 1998; Govers et al., 1999; Bird et al., 2007; Bhandari et al., 2009), and the expression of genes involved in proton-linked transport of monocarboxylates and glucose homeostasis (Haenen et al., 2013).

The major health boosting effect of RS is modifying and stabilising intestinal microbiota and increasing the expression of genes responsible for gut development through the production of SCFA which lowers pH in the colon and creates an acidic and hostile environment to the harmful microbes and prevent their overgrowth (Roy et al., 2006). Acetate, propionate, and butyrate are the major SCFA produced in the colon, of which butyrate is thought to be most beneficial for gut health. Butyrate is the main energy source for the cells that line the colon (Elia and Cummings, 2007). Other health benefits associated with butyrate are the protection against mucosal oxidative stress, strengthening of the colonic defense barrier, and anti-inflammatory properties (Hamer et al., 2008).

In line with this, several studies have examined the potential of RS to improve gut health and function in swine and poultry. How the fermentation of RS increases the production of SCFA and stabilises gut microbiota, and results in healthy and functional gut is diagrammatically illustrated in Fig. 1.

Studies have examined the potential role of RS in improving gut health and function in swine and poultry. Supplementation of a corn-soybean meal-wheat-wheat middlings-based control diet with raw potato starch (RPS) at 0.5% or 1.0% daily for 28 days has been reported to improve fecal consistency and total cecal SCFA concentration and reduce ileal and cecal digesta pH in pigs weighing 7.2 kg (Heo et al., 2014). However, supplementation of RPS did not reduce the growth performance of piglets, showing RPS has the potential to enhance the characteristics of a functional gut in weaned pigs without adverse effects on growth. In another study, the effect of RPS with or without probiotics on SCFA concentration and fecal consistency and growth performance has been examined (Krause et al., 2010). The results of this study indicated that increased colonic digesta SCFA concentration and fecal consistency in pigs fed diets containing 14% RPS compared with pigs fed non-RPS diets. Although average daily gain was improved in pigs fed a diet containing a combination of RPS and probiotics, it was significantly reduced by supplementation of RPS alone, which could be attributed to reduced average daily FI in this group. This shows that although gut health can be improved by supplementation of RPS, growth may be impaired by the low FI, which can be explained by satiety inducing effect of RS (Sajilata et al., 2006; Da Silva et al., 2012). Therefore, developing a phase-wise feeding strategy where piglets can be supplemented with known amount of RS shortly after weaning might help to reduce the negative effect on growth.

In a study where the effect of RPS on the production of SCFA and intestinal morphology has been investigated in pigs weaned at 4 weeks of age (Hedemann and Knudsen, 2007), pigs fed 160 g/kg RPS had the longest villi whereas those fed 80 g/kg of RPS had the deepest crypts. Additionally, villous height at the mid-small intestine and average daily gain were positively correlated, and colon weight and the proportion of butyric acid increased with increasing amount of RS (Hedemann and Knudsen, 2007). Moreover, in a study where the effect of RPS originated from 2 types of potato (*Tuberosum* and *S. Phureja*) on histomorphology was examined, birds fed RPS had significantly higher duodenal and jejunal villus to crypt ratio compared to birds that fed a control diet without RS, showing the potential of RS to improve gut structure (Ariza-Nieto et al., 2012).

Although the health benefit of RS1, 2, and 3 have been extensively investigated (Birt et al., 2013; Singh et al., 2010), chemically modified RS or RS4 is also gaining attention because of the possibility to control reduction in starch digestibility by targeted modification of the starch molecule. For example, the results of a study that examined the efficacy of acetylated high amylose maize starch and butyralated high-amylose maize starch in broilers challenged with necrotic enteritis have indicated that birds that fed the 2 forms of maize starch had higher body weight gain at 24 and 35 days compared with control birds (M'Sadeq et al., 2015). This improved growth performance can be explained by improvement in gut health and function, because birds fed butyralated high-amylose maize starch had increased jejunal villus height to crypt depth ratios and increased acidity in the gut, which may reduce the growth of pathogenic microorganisms. Creation of an acidic environment is attributed to increased production of SCFA, because ileal and caecal butyrate levels were higher in birds fed acetylated high-amylose maize starch (SA) and butyralated high-amylose maize starch (SB) supplemented diets (M'Sadeq et al., 2015).

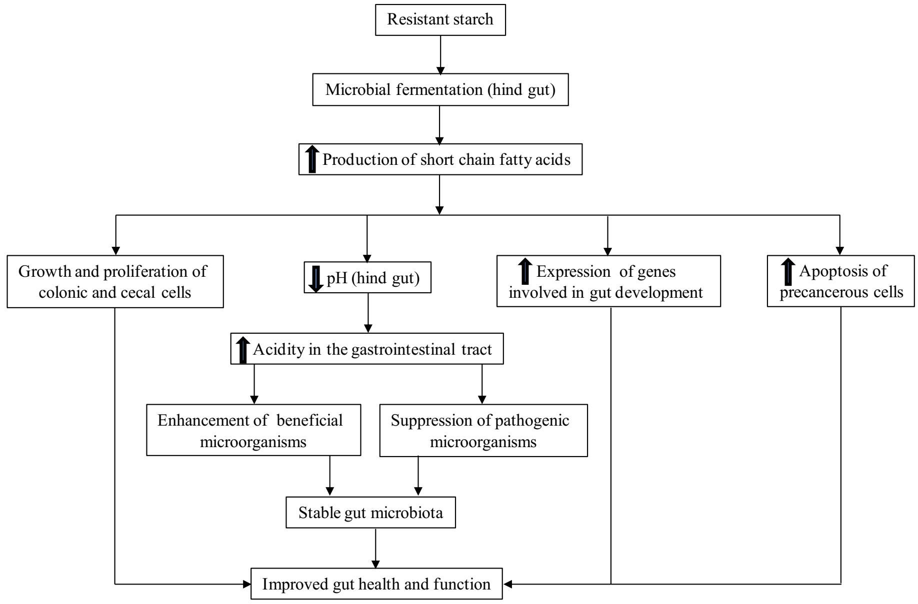

Fig. 1. Diagrammatic illustration of how resistant starch improves gut health.

2.2. Effects of resistant starch on gut microbial composition and nitrogenous metabolites

Addition of fermentable carbohydrates to the diet of weanling pig has been shown to promote bacterial diversity and stabilisation of the microbiota (Konstantinov et al., 2004). It increases the relative abundance of *Lactobacilli* in the small intestine and the stability and diversity of the bacterial community in the colon (Konstantinov et al., 2004). Bacterial species that will be favoured due to RS feeding could also depend on RS type. For instance, model colonic fermenter systems employed to determine bacterial groups using specific substrates indicated that the bacterial composition and production of SCFA are substrate dependent (Castillo et al., 2007; Duncan et al., 2003). This is consistent with the notion that each type of RS has the potential to modify the relative composition of gut microbial community due to the preferential substrate-binding abilities of the bacteria (Flint, 2012; Martinez et al., 2010). For instance, RS2 increases the fecal abundance of important butyrate producing *Ruminococcus bromii* and reduces the abundance of *Eubacterium rectale*, whereas RS4 increases *Bifidobacterium adolescentis* and *Parabacteroides distasonis* (Martinez et al., 2010). In a comprehensive microbial characterization of cecal samples obtained from growing pigs fed diets containing RS4, the relative abundance of *Ruminococcus, Parasutterella*, *Bilophila, Enterococcus*, and *Lactobacillus* were reduced, whereas the abundance of *Meniscus* and *Actinobacillus* was increased (Metzler-Zebelia et al., 2015), showing the potential effect of the chemical structure of RS on the relative abundance of microbial species.

Sun et al. (2015) also investigated the effects of long-term intake of raw potato starch (RPS) on microbial composition and gene expression profiles in the colon of pigs. Whereas the relative abundance of *Turicibacter, Blautia, Ruminococcus, Coprococcus, Marvinbryantia, and R. bromii* related in colonic digesta and mucosa was increased, the relative abundance of *Clostridium, Treponema, Oscillospira, Phascolarctobacterium*, RC9 gut group, and S24-7-related operational taxonomic units was reduced by feeding a RPS-supplemented corn-soybean-based diet. Higher relative abundance of *Ruminococcus* species in the digesta of pigs fed RPS reflects improvement in butyrate production and gut health (Pryde et al., 2002), and the digestibility of fiber and RS plays a primary role in the degradation of these dietary components (Flint et al., 2008; Chassard et al., 2012). Similarly, the improved relative abundance of *Coprococcus* that belongs to the *Clostridium coccoides* cluster in the digesta of pigs fed RPS diet might be related to improved butyrate production as they have been linked with the production of this metabolite in human colon (Louis and Flint, 2009). Feeding of RPS diet also decreased pH in the colon contents, resulting in the increased production of SCFA by microbial fermentation of starch (Fang et al., 2014), and reduction of pathogenic microorganisms (Haenen et al., 2013).

Examination of the effects of a diet on luminal microbiota composition, luminal SCFA concentrations, and the expression of host genes involved in SCFA uptake and signaling, and satiety regulation in mucosal tissues of small intestine, cecum, and colon has shown healthy gut-associated butyrate-producing *Faecalibacterium prausnitzii*, but reduced relative abundance of potentially pathogenic members of the *Gammaproteobacteria*, including *Escherichia coli* and *Pseudomonas* spp. in pigs fed diets contained high RS (Haenen et al., 2013).

The potential of butyrate to reduce the growth of common pathogenic organisms in poultry also has been evaluated in different experiments. For instance, in an experiment conducted to examine the efficacy of butyrate to reverse the dysbiotic effect of coccidian, birds received butyric acid before coccidial oocyte challenge showed higher growth rate following the challenge compared with birds received non-medicated feed (Leeson et al., 2005). This improved growth performance can be explained by the improved gut health due to butyrate treatment. Similarly, coated butyric acid significantly decreased cecal *Salmonella Enteritidis* colonization at 3 d post infection in young chickens compared with control birds (Van Immerseel et al., 2005) and butyrate-based additives showed a significant reduction of *Salmonella Enteritidis* infection in 1-d-old broiler chickens after 27 days of feeding in a 42-day trial (Fernández-Rubio et al., 2009).

Resistant starch also has the potential to reduce harmful nitrogenous metabolites that are produced as a consequence of feeding diets high in crude protein (Magee et al., 2000; Mu et al., 2016). These protein fermentation products associated with toxic and proinflammatory impact on the intestinal epithelium (Hampson, 1994; Sørensen et al., 2009). To this end, the effect of RS on protein fermentation and concentration of SCFA has been studied recently using *in vitro* cultivation of inocula from the large intestine of pigs (Xiangyu et al., 2017). The data showed that concentrations of SCFA were significantly increased whereas ammonia nitrogen and branched-chain fatty acids, which indicate protein fermentation, decreased as the levels of corn RS increased. Additionally, the counts of total bacteria, *Bifidobacterium* and *Lactobacillus* were significantly increased with increased levels of corn RS (Xiangyu et al., 2017). In one study, long-term intake of RPS diets increased crude protein and mucin contents in the colons of pigs and decreased total amino acids, ammonia-nitrogen, tryptamine, tyramine, branched-chain fatty acid, phenol, cresol, indole, and skatole concentrations when compared with corn starch diets (Zhou et al., 2016).

2.3. Effects of resistant starch on the expression of transcripts in the gut

In addition to improving histomorphology and modifying and stabilising gut microbiota, RS increases the expression of intestinal genes that plays an important role in gut health. Analysis of the colonic transcriptome profiles in pigs revealed that RPS diets changed the colonic expression profile of genes that are involved in immune response and significantly increased the expression of one of the pro-inflammatory cytokine, IL-1β, but suppressed the expression of genes involved in lysosome (Sun et al., 2015), suggesting that long-term intake of high amount of RS may have both positive and negative effects on gut health.

High dietary RS also increased the concentration of cecal and colonic SCFA and the cecal expression of monocarboxylate transporter 1 gene (*MCT1*) and glucagon in pigs (Haenen et al., 2013). Down-regulation of *MCT1* expression in the colon of piglets has been linked to bacterial protein fermentation and pro-inflammatory cytokine-mediated signalling (Tudela et al., 2015), and bacterial protein fermentation and pro-inflammatory cytokine expression have been associated with diarrhea in piglets (Prohaszka and Baron. 1980), showing the importance of this enzyme in maintaining gut health.

Similarly, colon expression of mucin genes (*MUC4, MUC5AC,* and *MUC12*) were significantly higher in pigs fed RPS than in those fed corn starch (CS) diet, suggesting the potential of long-term intake of RS diets to improve gut health by increasing mucin secretion and by reducing the harmful fermentation of protein (Zhou et al., 2016). However, the expression of these genes should be verified at protein level whether the corresponding metabolites are differentially expressed.

3. Factors affecting the fermentability of resistant starch and production of SCFA in pigs

Fermentation of RS and production of SCFA are time dependent. Pigs have appreciable capacity to ferment RS, and this capacity varies with the time and the age of the animal. Because of the progressive selection of starch-fermenting bacteria (Topping and Clifton, 2001; Haenen et al., 2013), fermentation of RS may be faster in pigs that have been exposed to RS for a long time (Martinez-Puig et al., 2003, 2007). Additionally, animals with a mature GIT ferment RS faster than growing animals. Several factors can affect the fermentability of RS including the source, amount, composition, and physical structure of RS entering large bowel (MacFarlane and MacFarlane, 2003) and microbial population during fermentation (Williams et al., 2001, 2005). Fermentability and factors affecting the fermentability of RS have been reviewed by Giuberti et al. (2015) and will not be reviewed here.

Fermentability of RS may also be influenced by the presence of other sources of dietary fiber. Specific fibers can distinctly affect digestive processes and therefore, digestibility and the fermentation of the complete diet may depend on fiber types present. Results of a study, that was conducted to evaluate the effects of readily fermentable fiber (β-glucans) and RS on nutrient digestibility and degradation of other dietary fibres in cannulated pigs (de Vries et al., 2016), have shown that the presence of β-glucans and RS altered digestion and fermentation of nutrients and fibers from other sources in the diet.

4. Effect of resistant starch on energy metabolism and growth performance

Fermentation of RS results in the formation of SCFA. Although it can cover up to 15% of the maintenance energy requirements in growing pigs (Bindelle et al., 2007), the conversion of SCFA into body energy is generally assumed to be less efficient than that of glucose (Bach Knudsen et al., 1993; Noblet et al., 1994). Research indicates that pigs may obtain as much as 30% of their energy requirements from SCFA-producing hindgut fermentation (Bergman, 1990). Energy utilization from RS has been subject to considerable debate. For instance, diets formulated to contain high retrograded maize starch have been associated with low digestible and metabolizable energy intake and energy retention in pigs (Gerrits et al., 2012). Consequently, increasing the proportion of fermentable starch at the expense of digestible starch may reduce energy efficiency (Zijlstra et al., 2012) and potentially impact nitrogen retention (Drew et al., 2012), fat metabolism (Yin et al., 2011) and the net portal appearance of amino acids (Li et al., 2008) in growing pigs with restricted access to feed. However, it is argued that this inefficiency may be compensated for by the gradual and prolonged supply of energy from the fermentation that potentially reduce energy expenditure for physical activities such as feeding motivation (Bolhuis et al., 2010; De Leeuw et al., 2008; Da Silva et al., 2012). It can also be argued that energy supply from fermentation of RS can cover the energy requirements for maintenance and reduce the portion of energy that would have been used for this purpose.

Depending on the source and the amount of RS in the diet, FI and feed efficiency, and growth performance in pigs may be variable. For example, Li et al. (2007) reported FI and feed efficiency and subsequently growth performance in barrows fed a diet containing 50% high amylose maize starch (RS2) were decreased compared with control pigs fed corn and digestible corn starch. Additionally, decreased glucose absorption has been reported in portal vein-catheterized pigs fed a diet containing high amylose starch (Regmi et al., 2011). However, growth performance measurements were nearly similar between growing pigs fed a diet containing 250 g/kg of corn starch and those fed 250 g/kg of RPS (Nofrarías et al., 2007). Moreover, daily intake of about 280 g of RS did not significantly reduce average daily gain and live weight at slaughter compared to other treatments in growing pigs (Pluske et al., 1998). These data are consistent with those of Doti et al. (2014) who reported similar growth performance traits and carcass characteristics in gilts fed diets containing 184 to 363 g/kg RS from cereal and legume grains. Whether the inconsistencies among the results from different studies could be attributed to differences in the amount of RS or the age of the animal needs further investigation.

5. Effect of resistant starch on carcass quality

Growth performance and carcass qualities are the most important traits for the profitability of the livestock industry. Although producers prefer to fast growing animals, post slaughter qualities of pork are of a considerable importance to the consumer and can affect the marketability of the product.

'Piggy' and unpleasant flavour of pork arise from skatole (Lundstroem et al., 1980; Bonneau et al., 2000). Skatole is the product of L-tryptophan metabolism by specialised bacteria in the colon (Yokoyama et al., 1977). This L-tryptophan originates from debris of gut mucosa cells in the distal part of the GIT but is not of dietary origin (Claus et al., 1994). Dose dependant reduction of skatole in the distal colon was reported in a study conducted to evaluate the effect of graded levels of RPS in barrows and gilts, showing the potential of RS to reduce piggy odour from pork (Loesel and Claus, 2005). Evidence exists that butyrate, fermentation product of RS, inhibits apoptosis of colon crypt cells *in vivo* so that less tryptophan from cell debris is available for skatole formation by microbes in the colon. Feeding potato starch containing high proportion of RS to growing pigs led to an increased fecal butyrate concentration and reduced apoptosis from 2.06 to 0.90 cells/crypt and consequently reduced skatole production (Claus et al., 2003). In another study, pigs fed barley-based diets had a lower indole concentration of another compound for piggy flavour in the adipose tissue compared with those fed the oat-based diet (Pauly et al., 2011).

In addition to health benefits, RS also improves the quality of carcass characteristics. For example, flare and belly fat concentrations were reduced from 159 to 20 ng/g fat and from 64 to 16 ng/g fat, respectively, in pigs fed graded levels of RS. However, no clear influence of RS was observed on carcass yield or carcass length and meat characteristics between pigs fed digestible and fermentable starch (Doti et al., 2014).

6. Conclusions and recommendations

Resistant starch is a fraction of dietary starch that escapes enzymatic digestion in the upper parts of the GIT and fermented by microorganisms in the hindgut. Fermentation of RS results in the production of SCFA, which reduces pH in the hind gut and creates an acidic environment that suppresses the growth of pathogenic microorganisms but enhances the growth of beneficial microbes. It also improves the characteristics of gut health and function. However, growth may be compromised when RS is supplemented for long time and/or in a large amount as energy production from SCFA is assumed to be less efficient than that from glucose. Therefore, determination of the ideal length of supplementation and the amount of supplemental RS may help to reduce growth depression and increase the use of RS as one of the alternatives for in-feed antibiotics.

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