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Chapter 6
Multi vs single application of enzymes to degrade fibre in diets for pigs

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Abstract

The largest quantities of fibre in most commercial diets for pigs originate from cereal grains and cereal grain co-products. The quantitatively most important fibre components in such diets are arabinoxylans and cellulose, which are poorly digested by endogenous and microbial enzymes in pigs. To increase fermentability of these components it is, therefore, necessary to add exogenous enzymes to the diets. Theoretically, four enzymes are needed to hydrolyse cellulose, whereas nine enzymes are needed to hydrolyse arabinoxylans. The greatest energy value of fermented cellulose will be obtained if cellulose can be fermented in the small intestine, but to achieve that, all four cellulose degrading enzymes need to be added to the diets. However, for arabinoxylans, the objective is not to achieve complete hydrolysis in the small intestine because absorbed pentoses do not contribute to the energy status of the pig. Instead, the objective is to hydrolyse arabinoxylans in the hindgut of pigs and microbial fermentation in the hindgut may be aided by addition of at least four enzymes to the diets. There are, however, only few studies with documented effects of addition of multiple enzymes to diets for pigs and more research in this area is needed.

Keywords: arabinoxylans, cellulose, enzymes, fibre, pigs

6.1 Introduction

The most common fibre fractions in cereal grains are cellulose and arabinoxylans, which contribute 25 to 30% and 50 to 60%, respectively, of the total fibre in most cereal grains and grain co-products (Jaworski *et al.*, 2015; Navarro *et al.,* 2019). Some cereal grains also contain mixed linked beta-glucans and other fibre components, but these are quantitatively less important than cellulose and arabinoxylans and mixed linked betaglucans are almost completely degraded by microbial enzymes in the intestinal tract with the majority of the degradation occurring in the small intestine (Graham *et al.*, 1989; Li *et al.*, 1996a). As a consequence, to significantly improve energy utilisation of fibre from cereal grains and cereal grain co-products, it is necessary to identify procedures to increase digestion or fermentation of cellulose and arabinoxylans. In pulse crops and oilseed meals, the main fibre components include cellulose and pectic polysaccharides, whereas no arabinoxylans are present in pulse crops and oilseed meals (Navarro *et al.*, 2019). Cellulose is a homopolysaccharide and arabinoxylans and pectic polysaccharides are heteropolysaccharides, but they all require

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multiple enzymes for complete hydrolysis. Many of the enzymes needed for fibre fermentation are expressed by the porcine hindgut microbiome, which results in partial, but not complete, breakdown of the fibres. The reason a complete hydrolysis is not obtained by the microbial enzymes is that they do not secrete all the enzymes needed for complete hydrolysis and there are certain barriers to fermentation that prevent microbial enzymes from reaching the target sites for hydrolysis. To increase energy utilisation from fibre by pigs, it is therefore, necessary that enzymes not secreted by the hindgut microbes in adequate quantities are supplied to the diets in a form that allow them to reach the target site in the intestinal tract and to be active in the intestinal environment. The present contribution will outline theoretical aspects of which enzymes are needed and how these enzymes theoretically may contribute to increased fibre hydrolysis. Because of the importance of fibre in cereal grains and grain co-products in swine nutrition, and because most commercial enzymes target cereal grain fibres, this review will be limited to discussing enzymes needed for hydrolysis of cellulose and arabinoxylans.

6.2 Enzymes needed to hydrolyse cellulose

Cellulose is a homopolysaccharide consisting only of glucose units that are linked by beta-1,4 glycosidic bonds in long chains that may contain up to 15,000 glucose units. In the crystalline part of cellulose, several glucose chains are linked by hydrogen bonds (Nishyiama *et al.*, 2002), which results in very tightly packed sheets of glucose units that are almost impossible to penetrate by enzymes and the crystalline parts of cellulose is, therefore, unfermentable (Ciolacu *et al.*, 2011). However, some parts of the cellulose chains are not linked by hydrogen bonds and these parts are known as the amorphous part of cellulose. The amorphous cellulose is less tightly packed than the crystalline cellulose because of the lack of hydrogen bonding, which allows for access of enzymes to the beta-1,4 bonds that link the glucose units. It is, therefore, possible that cellulose digesting enzymes may increase hydrolysis of cellulose.

For hydrolysis of amorphous cellulose, four enzymes are needed. These enzymes include endo-glucanase, exo-glucanase, cellodextrinase, and beta-glucosidase (Mansfield *et al.*, 1999; Zhang and Zhang, 2013). The endo-glucanase will hydrolyse beta-1,4 linkages in the middle of the amorphous cellulose chain of glucose units and generate oligosaccharides. The exo-glucanase will digest the glycosidic bonds between glucose unit one and two or between unit two and three from the reducing end or from the non-reducing end of the cellulose and generate oligosaccharides or disaccharides consisting of two to five glucose units. The final hydrolysis will be completed by the cellodextrinase and beta-glucosidase enzymes and individual glucose units will be released (Zorec, 2014). If this hydrolysis can be completed in the small intestine, glucose can be absorbed and metabolized in the body the same way as glucose from starch is utilised. If the hydrolysis takes place in the hindgut, the liberated glucose will be metabolized by the hindgut microbiome with a subsequent synthesis of short chain fatty acids that will be absorbed and metabolized for energy or lipid deposition.

The major challenges to cellulose fermentations are: (1) the inaccessibility of the beta-1,4 glycosidic bonds in the crystalline part of cellulose due to hydrogen binding between the glucose chains; (2) the lack of extensive quantities of cellulolytic microbes in the hindgut of pigs; (3) the slow activity of the beta-glucanases needed for cellulose hydrolysis; and (4) the

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relatively short retention time in the hindgut of pigs. It is possible to degrade the hydrogen bonds among the glucose chains in the crystalline part of cellulose via chemical treatments (Fahey *et al.*, 1993), but there are no enzymatic procedures to degrade these hydrogen bonds and the crystalline part of cellulose is, therefore, unfermentable in feed ingredients that have not been chemically treated. Fermentation of cellulose is, therefore, largely restricted to the amorphous part. Because of the potential to liberate glucose from amorphous cellulose, the greatest energy contribution may be obtained if hydrolysis of this part takes place in the small intestine, but due to the low concentration of microbes in the small intestine of pigs, the enzymes needed to hydrolyse amorphous cellulose need to be supplied in the diet. Like other feed enzymes, these enzymes will need to be able to survive the low pH in the stomach and be resistant to gastric and pancreatic proteases. In addition, due to the short transit time in the small intestine, cellulose degrading enzymes need to be able to act within 2 to 4 hours to liberate the glucose before the digesta leaves the small intestine. Because of the lack of substantial microbial enzymes in the small intestine, endo-glucanase, exo-glucanase, cellodextrinase and beta-glucosidase need to be supplied in the diet.

6.3 Arabinoxylan degrading enzymes

Arabinoxylan is a heteropolysaccharide that contains a xylose backbone and side chains of arabinose, galactose, and glucuronic acid (De Vries and Visser, 2001; Gamuf *et al.*, 2007). Some of the arabinose units in the side chains are esterified by coumaric acid or ferulic acid, which may link arabinoxylan to lignin. Lignification of arabinoxylan is mainly occurring in the plant cell wall (Bach Knudsen, 2014), whereas arabinoxylan in the endosperm generally is not lignified, but lignin is a major barrier for microbial enzymes and reduces fermentability of arabinoxylans. As a consequence, the unlignified arabinoxylan in the endosperm is more fermentable than the arabinoxylan in the cell wall (Glitsø *et al.*, 1999).

To fully hydrolyse arabinoxylans, a total of nine enzymes are needed. An endoxylanase is needed to hydrolyse the beta-1,4 bonds between the xylose units in the arabinoxylan backbone. To hydrolyse the bonds in the sidechains, de-branching enzymes such as beta-galactosidase, arabinoxylan arabinofurano-hydrolase, arabinofuranosidase, glucuronosidase, acetylxylan esterase, coumaroyl esterase, and feruloyl esterase are needed. During action of these enzymes, dimers or oligosaccharides of xylose from the xylose backbone are generated and a beta xylosidase is needed to hydrolyse these components into free xylose units. It is likely that microbial beta xylosidase will be effective in completing this final hydrolysis and the beta xylosidase enzyme therefore will not need to be added to the diet.

Unlike glucose units generated from hydrolysis of cellulose, xylose and arabinose that are the main monosaccharides in arabinoxylans, are pentoses, and therefore, not used in energy metabolism by pigs. As a consequence, absorption of these sugars from the small intestine will not contribute to the energy status of the animal and absorbed xylose and arabinose units are primarily excreted in the urine (Abelilla, 2018; Schutte *et al.*, 1991, 1992). It is, therefore, not the objective to generate free xylose and arabinose in the small intestine of pigs. Instead, the objective of providing exogenous enzymes to pigs is to hydrolyse enough of the bonds in arabinoxylans in the hindgut that the microbial enzymes can complete the

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hydrolysis, ferment the liberated sugars, and generate short chain fatty acids that may be absorbed from the hindgut of the pig.

Much of the focus of exogenous arabinoxylan degrading enzymes has been to provide endoxylanase that will hydrolyse some of the bonds in the xylose backbone and generate smaller oligosaccharides for microbial fermentation (Adeola and Cowieson, 2011). However, microbial enzymes are not believed to express sufficient quantities of the arabinofuranosidase enzyme, which is needed to hydrolyse the glycosidic bond between two arabinose units in a side chain (Glitsø *et al.* 1999). It may, therefore, be necessary to add the furanosidase enzyme as an exogenous enzyme to assist in the hydrolysis of arabinoxylans. In contrast, the arabinoxylan arabinofurano-hydrolase enzyme, which is needed to hydrolyse the glycosidic bond between the xylose in the backbone of arabinoxylan and the first arabinose unit in the side chain, is believed to be expressed in sufficient quantities by intestinal microbes, but this enzyme is only effective if the sidechain consists only of one arabinose unit. As a consequence, an exogenous arabinofuranosidase enzyme is first needed to hydrolyse bonds between adjacent arabinose units in the side chain and after the action of this enzyme when there is only one arabinose unit left in the sidechain, the microbial arabinoxylan arabinofurano-hydrolase will hydrolyse the bond between arabinose and xylose. It therefore appears that the arabinofuranosidase enzyme is critical for full fermentation of arabinoxylans.

Even more important are the coumaroyl esterase and the feruloyl esterase enzymes because these two enzymes hydrolyse the bonds between the sidechain arabinose and coumaric acid and ferulic acid, respectively. Because both of these phenolic acids allow for linking the sidechain to lignin, and because lignin hinders fermentation of the fibre, a complete hydrolysis of arabinoxylans is only achieved if the molecule is de-lignified. In addition, coumaric and ferulic acids reduce the action of endo-glucanases (Agger *et al.*, 2010) and therefore reduce microbial fermentation of cellulose (Snelders *et al.*, 2014). However, the two esterases needed to de-lignify arabinoxylans are not expressed by intestinal microbes. As a consequence, to improve fermentation of arabinoxylans, exogenous coumaroyl esterase and feruloyl esterase would need to be supplied in a form that allow these enzymes to separate coumaric acid and ferulic acid, and therefore also lignin, from the sidechain arabinose units.

6.4 Effects of multi enzyme addition to diets for pigs

Effects of non-starch polysaccharide degrading enzymes (NSPases) are thought to be a result of reduced viscosity in the intestinal tract, degradation of the plant cell wall, and formation of oligomers that have prebiotic properties (Bedford, 2018). However, much of the data behind these conclusions are based on poultry, and because reduced viscosity does not affect digestibility and absorption of energy or nutrients in pigs (Navarro *et al.*, 2018), it is unlikely that the viscosity effect is significant in pigs. That leaves the degradation of cell wall materials and generation of prebiotic substances as the two most likely reasons for improved growth performance of pigs fed diets containing NSPases. The prebiotic effects have been demonstrated in broiler chickens (De Maesschalck *et al.*, 2015; Morgan *et al.*, 2019), but at this time, there are no definitive reports in peer-reviewed publications from studies with pigs to demonstrate the prebiotic effect of fibre degrading enzymes. Because several enzymes are

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theoretically needed to hydrolyse cellulose and arabinoxylans in the intestinal tract of pigs, it is likely that addition of multiple enzymes are needed to obtain measurable increases in energy digestibility in pigs. To the best of the knowledge of this author, there are however, no reports from studies in which the four enzymes needed for increased cellulose hydrolysis were investigated. This is unfortunate because it is expected that the energetic advantage of hydrolysing cellulose in the small intestine will be greater than the advantage of hydrolysing arabinoxylans in the hind gut simply due to the greater energy value of glucose absorbed in the small intestine compared with arabinose and xylose that is fermented in the large intestine. Whether the lack of such published peer-reviewed papers is a result of difficulties in obtaining a positive response from adding cellulose degrading enzymes to diets for pigs or if it is because of difficulties in engineering such enzymes is unknown. But it is expected that any small intestinal hydrolysis of cellulose will increase the energy value of the diet.

There are, however, a number of reports from studies in which several enzymes aimed at increasing the hydrolysis of arabinoxylans. It is also possible that in some of the studies in which only addition of xylanase was reported, there may have been activity of other arabinoxylan degrading enzymes that were not known to the manufacturer of the enzyme, or just not declared (Bedford, 2018). In fact it is believed that very few purified enzymes are sold to the feed industry and the majority of enzymes sold are believed to have some side-activities that may or may not be known to the manufacturer of the enzyme (O'Neill *et al.*, 2014). In poultry, it was demonstrated that inclusion of arabinofuranosidase in addition to endo-xylanase resulted in improved performance (Ravn *et al.*, 2018). In a recent meta-analysis of studies with pigs, it was concluded that the apparent total tract digestibility of energy was not improved by addition of endo-xylanase to the diet, but if a complex of carbohydrases were used, a small, but significant, improvement in energy digestibility was observed (Torres-Pichard *et al.*, 2017). Thus, results of this meta-analysis as well as results of other experiments (Li *et al.*, 2019; Tiwari *et al.*, 2018; Tsai *et al.*, 2017) support the hypothesis that multiple enzymes are needed to obtain a positive response in digestibility. However, several studies have failed to observe a positive effect of using multiple enzymes (Agyekum *et al.*, 2015; Gdala *et al.*, 1997; Susenbeth, 2011). It is not surprising that different responses among studies are obtained because enzyme preparations, pig conditions, and feed manufacturing varies among studies. It is also important to define the cereal grain or grain co-product that is used because the same enzyme or enzyme complex may result in different responses in diets based on different cereal grains (Abelilla and Stein, 2019; Lærke *et al.*, 2015; Li *et al.*, 1996b). Different qualities or varieties of the same cereal grain may also react differently to addition of NSPases. It is also possible that different families of the same enzyme will result in different responses as has been demonstrated with xylanase from family 10 compared with xylanase from family 11 (Morgan *et al.*, 2017; Pedersen *et al.*, 2015). Thus, there are a number of factors that may influence responses to enzymes in diets for pigs, but at this time it is not known how these factors possibly influence responses. Although there are numerous studies in which beneficial effects of addition of a single endo-xylanase enzyme were observed, it is likely that improved effects will be observed, if a mixture of enzymes are used. At least theoretically, several enzymes that are not expressed by the hindgut microbiota in adequate quantities are needed for hydrolysis of arabinoxylans, and results from some *in vivo* studies support this concept.

6.5 Conclusions

The two main fibre components in cereal grains and cereal grain co-products are arabinoxylans and cellulose, whereas cellulose and pectic polysaccharides are the main fibre components in oilseed meals. Due to the greater inclusion rate of cereals and cereal co-products in diets for pigs compared with oilseed meals, the fibre fraction in diets for pigs are primarily defined by the fibre in the cereal grains and grain co-products used. Thus, to increase the energy contribution from fibre in pig diets, it is necessary that the degradation of cellulose and/or arabinoxylans increases. This may be accomplished by addition of feed enzymes to the diets, but it appears that for both cellulose and arabinoxylans, multiple enzymes may be needed to obtain a measurable increase in the energy contribution from fibre. Most focus has been placed on development of enzymes to degrade arabinoxylans and combinations of endo-xylanase, arabinofuranosidase, ferulic acid esterase, and coumaric acid esterase may be needed to obtain a significant response. However, the energy contribution from small intestinal degradation of cellulose will be greater than that of hindgut degradation of arabinoxylans. Thus, if enzymes for small intestinal degradation of cellulose can be successfully developed it will likely result in increased energy contribution to the pig. It is, however, acknowledged that even ruminant animals have a low degradability of cellulose so the challenges in identifying exogenous enzymes that can accomplish this in monogastric animals are significant.

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