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## Regulation of digestion kinetics in swine

### *Régulation de la cinétique de la digestion chez le porc*

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#### **Abstract**

Growing importance of upcycling agricultural and food processing byproducts through livestock production, increases the variation in the nutritional quality of feed ingredients. In addition to the extent, the kinetics of digestion can affect the metabolic fate of nutrients after absorption. Together with a growing body of evidence of interactions occurring in the lumen of the digestive tract, this urges the need for insights into the regulation of digestion kinetics. Results of recent studies on the regulation of digestion kinetics in swine will be presented and discussed, with a focus on digestion kinetics of starch and proteins, regulated by dietary fibres and particle size distribution. Whereas starch digestion kinetics are highly influenced by the starch source, the feed matrix, and can be accelerated by thermal treatment, digestion kinetics of proteins follows the sequential emptying of liquids and solids from the stomach. Typically, digesta liquids are emptied about 2 h faster from the stomach than solids, but this difference can be reduced by viscous, soluble fibres or enlarged by coarse particles ( $>0.3$  mm). Gastric mixing affects the pH gradient in the stomach and thereby likely the post-stomach hydrolysis rates. Dietary water binding capacity, but not dietary extract viscosity, appears to be a strong predictor of digesta phase separation in the stomach. Small intestinal digesta transit appears to be highly variable and difficult to influence through dietary properties. These insights can facilitate progress in feed ingredient evaluation and feed formulation in complex diets, provided that more information about ingredient properties is registered.

**Keywords:** starch, protein, dietary fibre, particle size, stomach

## Résumé

La valorisation des sous-produits issus de l'agriculture et de la transformation des aliments dans les fermes d'élevage entraîne une variabilité accrue de la qualité nutritionnelle des ingrédients utilisés dans l'alimentation animale. En outre, la cinétique de digestion peut influencer le devenir métabolique des nutriments après l'absorption. Compte tenu de l'accumulation des preuves d'interactions se produisant dans la lumière du tube digestif, il est crucial d'approfondir notre compréhension de la régulation de la cinétique de digestion. Les résultats d'études récentes sur la régulation de la cinétique de digestion chez les porcs seront présentés et analysés, en portant une attention particulière à la cinétique de digestion de l'amidon et des protéines, qui est influencée par les fibres alimentaires et la distribution de la taille des particules. La cinétique de digestion de l'amidon dépend principalement de la source de l'ingrédient, la matrice alimentaire, et peut être accélérée par un traitement thermique. En revanche, la cinétique de digestion des protéines est déterminée par la vidange séquentielle des liquides et des solides de l'estomac. En règle générale, les liquides sont évacués de l'estomac environ deux heures plus rapidement que les solides, mais cette différence peut être atténuée par la présence de fibres visqueuses et solubles ou augmentée par celle de particules grossières ( $> 0,3$  mm). Le brassage du contenu gastrique modifie le gradient de pH dans l'estomac, influençant vraisemblablement le taux d'hydrolyse en aval. Le pouvoir de rétention d'eau de l'aliment, plutôt que la viscosité de l'extrait, semble être un facteur de prédiction important de la séparation des phases du digesta dans l'estomac. Le transit du digesta dans l'intestin grêle semble être très variable et difficilement à modifier par les propriétés des aliments. Ces connaissances peuvent contribuer à améliorer l'évaluation des ingrédients alimentaires et la formulation des rations complexes, à condition de pouvoir recueillir davantage de données sur les propriétés des ingrédients.

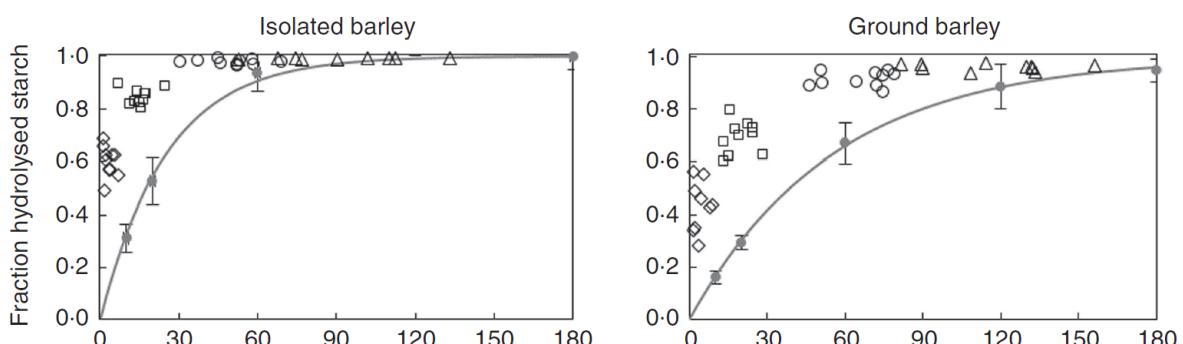
## Introduction

Upcycling of agricultural by-products, food waste, and food processing by-products through livestock production is of growing importance. Concomitantly, variation in type and nutritional quality of feed ingredients is increasing. Ingredients are commonly evaluated based on their measured extent of digestion, listed in feeding tables that provide the basis for diet formulation. Awareness increases that in addition to the extent, the kinetics of digestion affects the metabolic fate of nutrients after absorption. This includes its influence on feed intake patterns, synchrony of absorption of nutrients and synchrony between nutrient supply and demand. Together with a growing body of evidence of complex interactions occurring within the lumen of the digestive tract (see e.g. De Vries et al. (2016)), this urges the need of developing feed evaluation approaches that take this variation into account. For this purpose, mathematical modelling provides an excellent platform. To date, however, the application mathematical models in feed evaluation is limited by the use of complete feeds as the starting point in most models. Connection to alterations in feeding value of ingredients, or interactions occurring inside the digestive tract, require the use of feed ingredients rather than complete feeds as the starting points of simulations. A first step in this direction was accomplished by Schop et al. (2023). The limiting step in improving this type of models is an appropriate characterization of physico-chemical properties of feed ingredients and the way these impact on digesta transit and hydrolysis kinetics, particularly so in the proximal parts of the digestive tract. This paper

summarizes recent work in our lab on protein and starch digestion kinetics with a special role for dietary fibres.

## Starch digestion kinetics

Variation in starch digestion kinetics among sources of different botanical origin has been well-established, with intrinsic starch properties like increased concentration of A-type crystalline structure and short amylopectin side-chains increasing hydrolysis rates across botanic origins. Within botanic sources, variation in hydrolysis kinetics is mainly explained by other properties such as the amylose content and the number of pores on the starch granules (Martens et al., 2018). The matrix in which starch granules are embedded has a dominant and ingredient dependent effect on the rate of starch digestion. For example, Martens et al. (2019) compared the digestion kinetics of isolated starch with that of starch embedded in the raw ingredient. For barley, starch digestion of the isolated starch was 16 % points higher half way through the small intestine, and 4 % at the distal small intestine when compared with that of ground barley. For maize, the difference half-way through the small intestine was not observed, but at the distal small intestine, the starch digestibility of the isolated maize starch was 15% points higher compared with that of ground maize. These differences were assessed both by *in vitro* methods (based on Englyst) and *in vivo* by the use indigestible markers in a dissection study. Remarkable differences occurred between the *in vitro* and *in vivo* methodologies, particularly so in the proximal small intestine. This difference is illustrated for isolated and ground barley in Figure 1.



**Figure 1.** Digestion kinetics of barley starch *in vitro* and *in vivo* in pigs. Digestion coefficients of starch measured in digesta recovered from part 1 (♦), 2 (□), 3 (○) and 4 (Δ) of the small intestine in pigs fed diets containing starch isolated from barley or as ground barley, plotted against the cumulative retention time. Symbols (●) indicate the average of in triplicate measured values of *in vitro* starch hydrolysis against incubation time; lines represent the first-order kinetic model fitted to the data points. Error bars represent the standard deviation of *in vitro* measured starch digestion (source: Martens et al. (2019)).

The comparison between the *in vitro* and *in vivo* estimates of starch hydrolysis kinetics illustrates the limitations of the *in vitro* methodology to adequately represent occurrence of starch disappearance in the very proximal small intestine. This points at an important role for the stomach. Further work with enzymes obtained from stomach extracts by Martens et al. (2020) highlighted the importance of salivary and bacterial amylases in initial solubilization of

starch, and appearance of small glucose polymers in the stomach. The importance of feed technologies to steer starch hydrolysis kinetics is obvious but not discussed here.

## Protein digestion kinetics

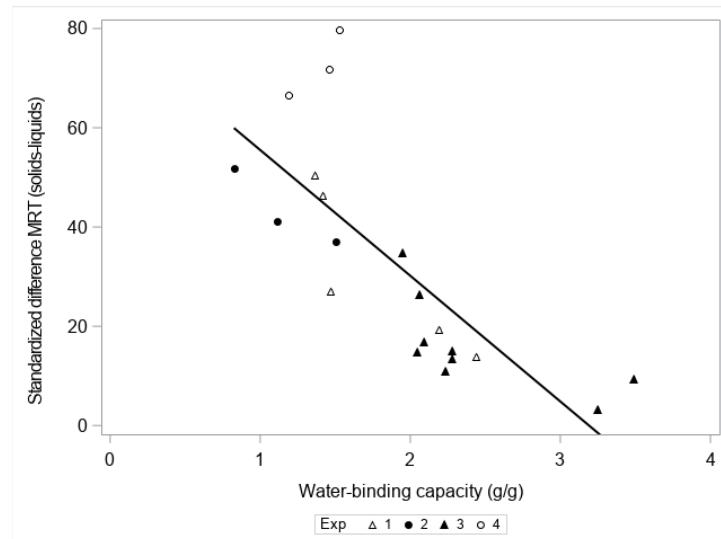
Data on digestion and absorption kinetics measured *in vivo* are scarce. The importance of variation in absorption kinetics of amino acids from the intestinal tract have been underpinned by portal blood appearance studies. While important, these are technically so demanding that between-study variation is large, and variation between protein sources scarce or unreliable. Milk proteins can be regarded as an exception. Modelling work of Le Feunteun et al. (2014) illustrates that variation in amino acid absorption kinetics of dairy proteins in minipigs is dominated by variation in stomach emptying processes. A similar conclusion was derived in the modelling work of Schop et al. (2023) in growing pigs. In a recent meta-analysis, (Dorado-Montenegro et al., 2025) estimated the difference in mean retention time between digesta solids and fluids in the stomach to be on average 1.5 hours, which is nearly 2/3 of the mean retention time of digesta in the entire small intestine. Based on this rather large difference, attention in *in vitro* studies of protein hydrolysis kinetics focuses on solubilization kinetics. Many research efforts concentrate on measurement of protein digestion kinetics *in vitro*, using techniques based on modifications to static protocols by Boisen and Fernández (1997) or INFOGEST (Brodkorb et al., 2019). The *in vitro* work of Chen et al. (2019) illustrates that considerable and relevant variation exists in N solubilization kinetics both during stomach and small intestinal incubation among feed ingredients. This was confirmed by unpublished work of Zhang in our group (Zhang, 2024) showing that the pattern of appearance of low molecular weight nitrogenous compounds largely followed patterns of N solubilization kinetics. She modified the Boisen & Fernandez procedure to include a pH gradient during stomach incubation. The major portion of N was solubilized and hydrolyzed, primarily following a drop in pH from 4 to 2 during incubation in the stomach, with large differences among ingredients. For example, solubilization rates for rapeseed meal, barley, peas and fishmeal were 0.1, 0.3, 0.3 and 0.1%/min during initial incubation at pH=4, respectively. This changed to 0.2, 0.1, 0.1 and 0.3/min during subsequent incubation at pH=2, respectively. In addition, the pH gradient itself contributes to altered N solubility. In the end, 46, 55, 68 and 73% of the N incubated solubilized in the stomach phase for rapeseed meal, barley, peas and fishmeal, respectively. This variation illustrates that measurement of solubilization kinetics *in vitro*, combined with understanding of pH gradients in the stomach and the regulation of stomach emptying are key to progress in this field.

## The role of dietary fibres

Dietary fibres have been shown to decrease the extent of digestion of dietary proteins. In a recent meta-analysis, Zhang et al. (2024) demonstrated that across databases, apparent ileal digestibility of proteins decrease by 0.6 to 0.7%-units per g/100g increase of total dietary fibre for cereal fibre sources and by 0.5 to 0.9%-units for non-cereal fibre sources. Mechanisms include entrapment of proteins in the fibre matrix, effects of physico-chemical properties of the fibre source and stimulation of endogenous protein losses. It is likely that the effects induced by dietary fibres do not only affect the extent, but also kinetics of the digestion process.

As discussed above, stomach emptying processes play a key role, simply by the gastric sieving process, causing a variable but substantial difference in the mean retention time of solids and

fluids in the stomach. The meta-analysis by Dorado-Montenegro et al. (2025) using data from 156 growing pigs fed one of 20 diets, revealed that 56% of the variation in digesta phase separation in the stomach was explained by dietary physico-chemical properties. The major portion of this variation was attributed to the water binding capacity of the diets (see Figure 2), and limited variation by other rheological parameters. Notably, extract viscosity of the diets explained no variation in digesta phase separation in the stomach, and none of the physico-chemical properties of the diets explained relevant variation in digesta transit in the small intestine. Determining the mean retention time of dietary fibres requires the use of dedicated tracers. Metals, mordanted to the fibre source of study can be useful in such tracer studies, particularly so in determining the effects of particle size. Using this methodology Sebastian et al. (2023), and (Lannuzel et al., 2024a; Lannuzel et al., 2024b), showed that the effects of particle size are source dependent. While increasing insoluble fibres clearly magnify digesta phase separation in the stomach (Sebastian et al., 2023), large particles of straw (Lannuzel et al., 2024a) and soybean hulls but not oat husks (Sebastian et al., 2023), remained longer in the stomach than their ground counterparts. Increasing gelating properties of the diet by including soluble fibre sources typically decrease digesta phase separation in the stomach (Lannuzel et al., 2024b). Even though fibre sources in animal nutrition do not always contribute to the supply of proteins and starch substantially, by altering digesta passage kinetics, they can act as key-regulators of nutrient absorption kinetics.



**Figure 2.** Association between digesta-phase separation in the stomach and the water binding capacity of 20 diets fed in 4 experiments. Difference in mean retention time (MRT) is expressed as  $(MRT_{solids} - MRT_{liquids}) / (MRT_{solids} + MRT_{liquids}) * 100$  of gastric digesta;  $r = -0.76$ ,  $P < 0.001$ ; Data from Dorado-Montenegro et al. (2025).

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