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Whole digesta properties as influenced by feed processing explain variation in gastrointestinal transit times in pigs

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Abstract

Physicochemical properties of diets are believed to play a major role in the regulation of digesta transit in the gastrointestinal tract. Starch, being the dominant nutrient in pig diets, strongly influences these properties. We studied transport of digesta solids and liquids through the upper gastrointestinal tract of ninety pigs in a 3 × 3 factorial arrangement. Dietary treatments varied in starch source (barley, maize and high-amylose maize) and form (isolated starch, ground cereal and extruded cereal). Mean retention times (MRT) of digesta solids ranged 129–225 min for the stomach and 86–124 min for the small intestine (SI). The MRT of solids consistently exceeded that of liquids in the stomach, but not in the SI. Solid digesta of pigs fed extruded cereals remained 29–75 min shorter in the stomach compared with pigs fed ground cereals ($P < 0{\cdot}001$). Shear stress of whole digesta positively correlated with solid digesta MRT in the stomach (r 0·33, $P < 0{\cdot}001$), but not in the SI. The saturation ratio (SR), the actual amount of water in stomach digesta as a fraction of the theoretical maximum held by the digesta matrix, explained more variation in digesta MRT than shear stress. The predictability of SR was hampered by the accumulation of large particles in the stomach. In addition, the water-holding capacity of gelatinised starch leads to a decreased SR of diets, but not of stomach digesta, which was caused by gastric hydrolysis of starch. Both of these phenomena hinder the predictability of gastric retention times based on feed properties.

Key words: Gastric emptying: Digesta passage behaviour: Growing pigs: Extrusion: Starch

Pig performance is affected by the rate of nutrient appearance in the portal vein. For example, pigs fed diets rich in rapidly digestible starch have shorter inter-meal intervals and meal durations(1) and greater activity-related energy expenditure(2), compared with pigs fed slowly digestible or resistant starch. Additionally, feeding pigs free lysine, which is rapidly absorbable, leads to a greater oxidation of essential amino acids compared with feeding protein-bound lysine(3). The rate of nutrient absorption is affected mostly by the rate of hydrolysis in combination with digesta transport, especially through the stomach and proximal small intestine (SI)(4). The rate at which digesta are transported through those organs is, in turn, affected by several mechanisms and meal properties, such as meal size(5), energetic content(6) and nutrient-activated feedback mechanisms(7,8). Moreover, digesta transport depends on the composition and properties of digesta. Typically, digesta are complex particulate suspensions, which change continuously upon transfer through the gastrointestinal tract (GIT)(9). Whole digesta consists of a soluble fraction and an insoluble particle fraction that travel at different speeds through the GIT(10,11). Consequently, nutrient absorption kinetics depend on the solubility of nutrients. Transit behaviour of whole digesta can be characterised by measuring the rheological properties of digesta, which depend on several basic chemical and physical properties of both the solid and liquid fractions. For example, rheological properties of whole digesta depend on the DM content, concentrations of soluble and insoluble polymers, liquid fraction viscosity and several properties related to the particular matter, such as its size distribution, water-holding capacity (WHC) and deformability(9,12–15). These properties

Abbreviations: EA, high-amylose maize starch in extruded form; EB, barley starch in extruded form; EM, maize starch in extruded form; GA, high-amylose maize starch in ground form; GB, barley starch in ground form; GIT, gastrointestinal tract; GM, maize starch in ground form; HA, high-amylose; HPSEC, high-performance size exclusion chromatography; IA, high-amylose maize starch in isolated form; IB, barley starch in isolated form; IM, maize starch in isolated form; MRT, mean retention time; SI, small intestine; SI4, terminal 1·5 m of the small intestine; SR, saturation ratio; WHC, water-holding capacity.

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can affect the mean retention time (MRT) of various digesta fractions. For example, large particles (>1–2 mm) remain in the human[16,17] and canine[18] stomach until they are broken down to smaller particles, thereby increasing the gastric retention time of digesta solids. In addition, a high viscous liquid fraction of digesta reduces solid digesta passage rates in humans[19] and pigs[20] in the upper GIT. Data on the relation between whole digesta rheology and its underlying properties, however, are scarce, and relations between whole digesta properties and transport are poorly understood[10,12,21].

Starch, in many pig diets provided in the form of cereals, is quantitatively the most important macronutrient and typically represents 40–50 % of the diet[22]. The form in which starch is presented to the pig is therefore one of the main determinants of rheological properties of diets. For example, feed processing, such as pelleting or extrusion, typically results in fractions of gelatinised starch[23,24], which increases the liquid fraction viscosity[25]. In addition, rheological properties of non-hydrothermal treated diets are affected by milling conditions, as the particle size distribution and shape affect the maximum packing density of solids in the particulate suspension, which in turn affects digesta viscosity[9]. In the present study, we assessed digesta passage behaviour throughout the upper GIT of pigs fed one of nine diets, varying in starch form and source. In addition, we studied relationships between whole digesta rheology and digesta MRT. The correlation between rheology and MRT was further explored by examination of underlying physical digesta properties. Lastly, we investigated the prediction of stomach digesta properties based on feed properties.

We hypothesised that whole digesta rheological properties would explain a major fraction of variation in digesta MRT. Hydrothermal processing of cereals by extrusion will lead to starch gelatinisation and a reduction in average particle size. The first is expected to increase digesta MRT in pigs, whereas the latter is expected to decrease MRT. The net effect therefore remains unknown.

Materials and methods

Experimental design, animals and diets

The experiment described in the present paper was part of a larger study on starch digestion kinetics, which is described in detail elsewhere[26]. The experiment was approved by the Dutch Central Committee of Animal Experiments under the authorisation number AVD260002016550. Briefly, ninety crossbred gilts (Topigs 20 × Pietrain sire), weighing 23·1 (SD 2·0) kg, were assigned to one of the nine dietary treatments in a 3 × 3 factorial arrangement, in four successive batches. Factors were starch source (barley, maize and high-amylose (HA) maize) and form (isolated starch, ground cereal and extruded cereal). The resulting dietary treatments were: barley starch in isolated (IB), ground (GB) and extruded (EB) forms; maize starch in isolated (IM), ground (GM) and extruded (EM) forms and HA maize starch in isolated (IA), ground (GA) and extruded (EA) forms. In total, ninety-six pigs were used: ten pigs were assigned per dietary treatment, whereas the remaining animals served as reserve animals and were used to replace excluded animals. Fourteen pigs were excluded due to a low feed intake: pigs that were excluded in one of the first three batches were replaced in the sequential batch. Replacement was done in such a way that a minimum of seven observations was realised for each dietary treatment. The experiment consisted of an adaptation period of at least 2 d, followed by an experimental period of at least 12 d, during which the experimental diets were fed. Pigs were housed in groups of four animals per pen but fed individually at 2·0 × the energy requirements for maintenance (750 kJ net energy per kg body weight$^{0·60}$)[27], divided over two equal meals at 08.00 and 16.00 hours. All the diets were mixed with water just before feeding. In the first batch, all diets were mixed with water to a feed:water ratio of 1:2. After the first batch, the feed:water ratio of ground diets was altered to 1:1·5 to facilitate ingestion. Pigs always had free access to water. During the last 2 d of the experimental period, the daily allowance of the pigs was equally divided over six meals, starting at 07.00 hours and applying a between-meal interval of 3 h, to reach a constant passage rate of digesta through the GIT. Just prior to dissection, a frequent feeding procedure was applied to enable the measurement of digesta passage kinetics: Each pig was fed six meals containing 1/12th of their daily allowance each, applying a 1-h between-meal interval. The first of the six hourly meals was fed exactly 6 h before a pig was euthanised. Pigs were euthanised and dissected in an order balanced for dietary treatment and time after onset of the frequent feeding procedure. Upon the start of the frequent feeding procedure of the first pig, extra meals (1/12th of daily feed allowance) were provided with 2-h intervals to the pigs whose frequent feeding procedure had not yet started, to prevent restlessness in the barns. Diets were formulated to meet or exceed the nutrient requirements of growing pigs[27] and designed to contain about 400 g starch per kg dry feed. All diets were formulated to be identical in crude protein, fat and total dietary fibre content, using soyabean meal, soyabean hulls, soyabean protein isolate, soyabean oil and sugar beet pulp. Details on ingredients, production conditions and the analysed composition are described elsewhere[26]. Cr and Co were included as markers in the feed at a level of 170 mg/kg to study digesta passage behaviour of solid and liquid digesta fractions, respectively. Cr was included in the form of chromium oxide (Cr_2O_3) and Co was included in the form of Co-EDTA.

Digesta collection

Prior to dissection, pigs were sedated and exsanguinated as described in detail elsewhere[26]. Immediately after exsanguination, clamps were placed between gastrointestinal sections to prevent the movement of digesta and the GIT was carefully removed. The stomach content was homogenised by manual mixing, and after recording the total weight and the pH, samples were collected. One representative sample was immediately frozen and kept at −20°C until freeze-drying, whereas another sample was kept at 4°C pending rheology and particle size analyses. The SI was carefully spread on a table and divided with clamps in four segments. The last 1·5 m from the SI (SI4) was considered to represent the terminal ileum. The rest of the SI was divided in three parts with equal length (SI1, SI2 and SI3, from proximal to distal SI). All parts were dissected, and their contents were collected by gentle stripping after which digesta of each part were manually homogenised. The total weight of the digesta was recorded, and a representative sample was immediately frozen and kept at −20°C until freeze-drying. In addition, samples from SI2 and SI4 were taken and stored at 4°C pending rheology and particle size analyses.

Chemical, physical and rheological analyses

Prior to chemical analyses, feed and freeze-dried digesta samples were ground to pass a 1 mm sieve using a centrifugal mill at 12 000 rpm (ZM200; Retsch). All analyses were performed in duplicate, unless indicated otherwise. DM content of digesta was determined in singlicate by recording the weight before and after freeze-drying. DM content in feed was determined according to NEN-ISO 6496[28].

Viscosity of digesta was measured using stress-controlled rheometers (MCR 301/MCR 502, Anton Paar GmbH) in samples (<48 h after digesta collection, stored at 4°C), without separation of the liquid and solid fraction and without grinding the samples, at 39°C. Samples were analysed as described previously[15], with slight adjustments. Briefly, feed samples were analysed after soaking the feed for 1 h in the feed:water ratio as fed from batch 2 onwards (1:2 for diets with isolated starch and extruded cereals, 1:1·5 for diets with ground cereals). A parallel plate profiled geometry (PP25/P2) of 25 mm diameter with a ribbed surface was used to avoid slip, and a plastic lid was used to avoid evaporation. For small intestinal digesta samples, harvested from the second and last part of the SI, the apparent viscosity curve was measured using a frequency sweep (100–1 Hz log). Feed and stomach digesta had both solid and liquid properties. To ensure permanent contact and confinement pressure, those samples were subjected to an oscillatory frequency sweep (from 275 to 1 Hz) at normal force controlled gap distance (0·5 N) and a constant strain (10 %). Settings were optimised based on the sample that had visually the highest gel strength, which was stomach digesta originating from pigs fed diets with isolated starch. For stomach digesta recovered from pigs fed EB or EM, the gel strength was not sufficient to remain a constant normal force controlled gap distance. Therefore, samples were subjected to the oscillatory frequency sweep at a fixed gap distance (2 mm). With the oscillatory measurements, we identified the shear stress, storage modulus (G') and loss modules (G'') at a frequency of 1 Hz, as previous research suggested that the forces naturally applied by the GIT are close to this frequency[29–31].

Particle size of digesta was analysed at 20°C in samples that were stored at 4°C or −21°C. Feed samples were analysed after soaking for 1 h in the feed:water ratio as fed from batch 2 onwards (1:2 for diets with isolated starch and extruded cereals, 1:1·5 for diets with ground cereals). Particle size was measured by laser diffraction (Mastersizer 3000; Malvern) using demineralised water as a dispersant. The reference material was wood flour (refraction index 1·53, absorption index 0·1, as supplied by the manufacturer), and each sample was analysed at least in triplicate. Measurements were performed in the range of 0·01–3500 µm. For further analyses, the volume percentage of particles was summarised in three classes: small particles, between 3·5 and 35 µm; medium particles, 35–350 µm and large particles, 350–3500 µm.

WHC of diets and freeze-dried digesta was determined in ground material using Baumann's apparatus[32]. A total of 105 (SD 6) mg of ground and freeze-dried samples was placed on a filter disc of 40 mm diameter with 10–16 µm pore size (Duran group). The volume of water absorbed to hydrate the sample until saturation was recorded and corrected for the amount of water that evaporated in this time, which was determined using a filter disc without sample.

Cr and Co concentrations were measured in singlicate by inductively coupled plasma optical emission spectroscopy. Cr and Co were measured at 357·9 and 228·0 nm, respectively, according to Van Bussel *et al.*,[33] after sample preparation according to Williams *et al.*[34]

Molecular weight distributions of the soluble fractions of feed and digesta were analysed with high-performance size exclusion chromatography (HPSEC). Digesta from all pigs within a dietary treatment were pooled by mixing equal weight aliquots of freeze-dried digesta of each pig. Freeze-dried and ground diets and pooled digesta were boiled in water for 5 min (50 mg/ml) and subsequently centrifuged. Supernatant was analysed using an Ultimate 3000 HPSEC system (Thermo Fisher Scientific). A set of four TSK-Gel columns (Tosoh Bioscience) was used in series: one guard column (6 mm inner diameter × 40 mm) and the columns super AW4000, 3000 and 2500 (6 mm inner diameter × 150 mm). The column temperature was set to 55°C. A volume of 10 µl of sample was eluted with filtered 0·2 M $NaNO_3$ at a flow rate of 0·6 ml/min, and the elution was monitored by refractive index detection (Shodex refractive index 101; Showa Denko K.K.).

Calculations and statistical analyses

The MRT of solid and liquid fractions of digesta was calculated based on quantities of Cr and Co recovered in GIT segments, assuming that hourly feeding induced steady-state conditions, according to Equation 1[35]:

$$\mathrm{MRT}(n) = (300 \times [\mathrm{marker}] \times W)/I \qquad (1)$$

Where MRT is the mean retention time in minutes in compartment n of the GIT; [marker] is the marker (Cr or Co) concentration in the digesta (mg/g DM); W is the weight of the dry intestine content (g DM) and I is the marker intake over 300 min prior to dissection (mg). ΔMRT was calculated as digesta MRT of solids minus the digesta MRT of liquids at each GIT compartment.

The power law model was used to model the apparent viscosity of small intestinal digesta, per pig per segment, measured over a range of shear rates (Equation 2)[36]:

$$\text{Apparent viscosity} = K \times \text{shearrate}^{(n-1)} \qquad (2)$$

where K is the consistency coefficient (Pa*s^n), which reflects the shear stress at a shear rate of 1/s, and n is the flow behaviour

Table 1. Mean retention times (MRT, min) of solid and liquid fractions of digesta recovered from the stomach and the small intestine (SI) of pigs fed diets containing barley, maize, or high-amylose maize starch, included as isolated powder, ground cereal, or extruded cereal*†
(Least-squares means and pooled standard deviations)

	Experimental diets												
	Barley			Maize			High-amylose maize				*P*‡		
	Isolated	Ground	Extruded	Isolated	Ground	Extruded	Isolated	Ground	Extruded	Pooled SD	Form	Source	Form × source
Max obs§	10	10	9	10	10	9	7	7	10				
Digesta solids													
Stomach	161	197	129	225	221	146	190	221	192	66	0·008	0·062	0·437
SI1	7	8	5	8	8	5	7	5	7	4	0·394	0·691	0·594
SI2	15	25	22	21	23	17	27	27	22	11	0·201	0·196	0·496
SI3	46	63	43	53	45	56	43	48	59	14	0·355	0·969	0·004
SI4	21	29	24	18	28	34	33	39	30	14	0·129	0·053	0·302
Total SI	86^{b}	124^{a}	94^{a,b}	100^{a,b}	102^{a,b}	111^{a,b}	109^{a,b}	120^{a,b}	116^{a,b}	22	0·024	0·073	0·039
Digesta liquids													
Stomach	132	127	130	187	159	131	171	164	137	55	0·132	0·089	0·652
SI1	7	7	5	9	8	4	7	5	6	5	0·071	0·7349	0·7402
SI2	18	24	21	22	24	16	29	29	25	11	0·278	0·049	0·793
SI3	61	78	52	67	56	70	53	67	70	20	0·532	0·977	0·014
SI4	28	35	24	23	33	36	38	51	37	18	0·148	0·025	0·513
Total SI	111	143	101	121	118	125	127	152	137	30	0·060	0·038	0·108

a,b When an interaction between form and source was found ($P < 0·05$), unlike superscript letters indicate significant differences between dietary treatment combinations ($P < 0·05$).
* MRT are estimated based on quantities of Cr (solids) and Co (liquids) recovered from digesta.
† SI4 is the terminal 1·5 m of the SI, whereas the rest of the SI is divided in three parts with equal length (SI1, SI2 and SI3, from proximal to distal SI, respectively).
‡ *P*-values for fixed effects of starch form (isolated, ground and extruded), source (barley, maize and high-amylose maize) and the interaction between form and source, analysed per segment.
§ The maximum number of replicate observations (obs) equals the number of replicate animals per dietary treatment. In some segments, not enough digesta was present to allow chemical analysis, causing one missing observation in SI1 of GB, SI1 of EA, SI4 of IB, and SI4 of GM, and two missing observations in SI1 of EM.

index, which is dimensionless and reflects the closeness to Newtonian flow. K and n were estimated by nonlinear regression procedures (PROC NLIN, SAS, version 9.4, SAS Institute).

To characterise the rheological properties of diets and stomach digesta, tanδ was calculated according to Equation 3[37]:

$$tan\delta = \frac{\text{Loss modulus}}{\text{Storage modulus}} \tag{3}$$

where loss and storage moduli were measured at 1 Hz.

From the DM content and WHC of diets and digesta, we calculated the saturation ratio (SR). The SR is the digesta water content, as fraction of the theoretical maximum of water that can be held by the DM according to its WHC. The SR was calculated according to Equation 4:

$$\text{SR} = \frac{\text{Water content}}{\text{Max water held}} \tag{4}$$

Where the water content is the percentage of water in the dietary or digesta suspension and max water held is the amount of water that can maximally be held in the dietary or digesta suspension, calculated as the DM content times WHC. For diets, the water content represents the water content of diets after they were mixed with water, in the ratios applied prior to feeding. An SR < 1 indicates that less water is present in the stomach than the amount of water that can potentially be held by the amount of DM. An SR > 1 indicates that more water is present in the stomach than can be held by the digesta matrix, based on its WHC properties.

Effects of dietary treatments on MRT were tested using a general linear mixed model (PROC MIXED, SAS), with starch form, starch source and their interaction as fixed effects and batch as random effect. Least square means were compared after Tukey's adjustment for multiple comparisons. Correlation coefficients between whole digesta rheology parameters and MRT, and whole digesta rheology and physical properties, were estimated using Pearson's correlation procedure (PROC CORR, SAS). Data are presented as least squares (LS) means and pooled standard deviation of the mean (S) unless stated otherwise. A retrospective power analysis was performed to validate the sample size of the present study. Considering digesta MRT as the most important parameter, the power was evaluated using the variation in digesta MRT observed in the present study, by calculating the critical F-value for a two-sided a level of 0·05 and for the mixed model study design[38]. For the stomach and SI, a power >0·69 was reached on the main effect of starch form and a power >0·52 was reached on the main effect of starch source. For the form × source interaction, a power of 0·29 was reached for the stomach and a power of 0·72 was reached for the SI. Significance was assumed at $P \leq 0·05$, while a tendency was considered when $0·05 < P \leq 0·1$.

Results

Mean retention times of solid and liquid digesta

The MRT of solid stomach digesta was 29–75 min shorter for pigs fed extruded cereals, compared with pigs fed ground cereals ($P < 0·01$, Table 1). The inclusion of barley tended

Table 2. Difference between mean retention times of solid and liquid fractions of digesta (ΔMRT, min) recovered from the stomach and the small intestine (SI) of pigs fed diets containing barley, maize or high-amylose maize starch, included as isolated powder, ground cereal or extruded cereal†‡
(Least-squares means and pooled standard deviations)

	Experimental diets												
	Barley			Maize			High-amylose maize				P§		
ΔMRT	Isolated	Ground	Extruded	Isolated	Ground	Extruded	Isolated	Ground	Extruded	Pooled SD	Form	Source	Form × source
Max obs‖	10	10	9	10	10	9	7	7	10				
Stomach	$29^{a,b,c,d*}$	69^{a*}	-1^{d}	$38^{a,b,c,d*}$	$62^{a,b*}$	$15^{c,d}$	$19^{b,c,d}$	$57^{a,b,c*}$	$54^{a,b,c*}$	29	<0·0001	0·401	0·003
SI1	−1	1	1	−1	0	1	−1	0	1	2	0·004	0·808	0·776
SI2	−3	2	0	−1	−1	2	−2	−2	−3	6	0·544	0·375	0·476
SI3	−15*	−15*	−9*	−15*	−10*	−14*	−9*	−18*	−11*	9	0·444	0·994	0·186
SI4	−6*	−6*	1	−4	−5	−2	−6	−11*	−7*	8	0·115	0·117	0·559
Total SI	−25*	−18*	−7	−21*	−16*	−14*	−18*	−32*	−21*	14	0·065	0·168	0·126

a,b,c,d When an interaction between form and source was found, unlike superscript letters indicate significant differences between dietary treatment combinations ($P < 0·05$).
* Value differs significantly from 0 ($P < 0·05$).
† ΔMRT is calculated as MRT of the solid digesta fraction minus MRT of the liquid digesta fraction, which are estimated based on quantities of Cr and Co, respectively.
‡ SI4 is the terminal 1·5 m of the SI, whereas the rest of the SI is divided into three parts with equal length (SI1, SI2 and SI3, from proximal to distal SI, respectively).
§ *P*-values for fixed effects of starch form (isolated, ground and extruded), source (barley, maize and high-amylose maize) and the interaction between form and source, analysed per segment.
‖ The maximum number of replicate observations (obs) equals the number of replicate animals per dietary treatment. In some segments, not enough digesta was present to allow chemical analyses, causing one missing observation in SI1 of GB, SI1 of EA, SI4 of IB, and SI4 of GM, and two missing observations in SI1 of EM.

to reduce the MRT of both solids (35–39 min) and liquids (28–29 min) in the stomach, compared with maize and HA maize ($P < 0·1$). The effects of dietary treatment on the separation of digesta fractions in the stomach were studied by subtracting the liquid MRT from the solid MRT (ΔMRT, Table 2). Extrusion reduced the ΔMRT in the stomach of pigs fed barley and maize by 59 min on average, compared with diets containing ground cereals, which was not observed for pigs fed HA maize (form × source, $P < 0·001$).

In the SI, the MRT of solid digesta averaged 7 min in SI1, 22 min in SI2, 51 min in SI3 and 28 min in SI4 (Table 1). The cumulative MRT of solid digesta in the SI of barley fed pigs was longer for pigs fed starch in ground form (124 min) compared with pigs fed starch in isolated form (86 min), which was not observed for pigs fed maize and HA maize-based diets (form × source, $P < 0·05$). The MRT of liquid digesta exceeded that of solid digesta in the SI for all pigs, except those fed EB ($P < 0·05$, Table 2). The ΔMRT in the SI tended to be longer for pigs fed diets with ground cereals, compared with pigs fed extruded cereals ($P < 0·1$).

Rheological characterisation of feed and digesta

All experimental diets had a storage modulus that exceeded the loss modulus and, consequently, a tanδ between 0 and 1 (Table 3). Extrusion increased the dietary shear stress of barley diets by a factor 1·9 and maize by a factor 1·6, whereas this was only a factor 1·3 for HA maize.

Regardless of the diet fed, tanδ of stomach digesta was between 0 and 1. The shear stress of all isolated and ground diets increased upon ingestion, whereas it decreased upon ingestion for extruded diets, except for EA. Within pigs fed ground cereals, stomach digesta of pigs fed barley had a higher shear stress than those fed maize or HA maize (form × source, $P < 0·001$). The shear stress of stomach digesta was greater for pigs fed isolated and ground diets, than for pigs fed extruded diets, particularly for pigs fed barley and maize ($P < 0·001$).

For all dietary treatments, the SI digesta viscosity at 1/s, equalling K, increased from SI2 to SI4. For SI2, pigs fed IM had a higher digesta viscosity than pigs fed EM, which was not observed for pigs fed barley and HA maize (form × source, $P < 0·05$). Additionally, digesta viscosity of SI2 of pigs fed GA maize exceeded that of EA, whereas this difference was absent for maize and barley fed pigs (form × source, $P < 0·05$). In SI4, digesta of pigs fed isolated diets had a higher viscosity (on average 227 Pa*s, $P < 0·05$) compared with pigs fed ground (155 Pa*s) and extruded diets (140 Pa*s). Additionally, pigs fed GB tended to have a lower digesta viscosity in SI4 than pigs fed IB (form × source, $P = 0·08$).

Correlations between digesta mean retention time and rheology of diets and whole digesta

Dietary shear stress was negatively correlated with solid digesta MRT in the stomach (r −0·71, $P < 0·05$, Table 4). In the stomach, digesta shear stress was positively correlated with solid digesta MRT (r 0·33, $P < 0·001$), but not with liquid digesta MRT. In contrast, digesta viscosity in both SI2 and SI4 explained almost no variation in solid or liquid digesta MRT ($r < 0·10$, $P > 0·1$). To further unravel the correlation between digesta rheology and MRT, we examined underlying physical and chemical properties of diets and stomach digesta, but not of small intestinal digesta.

Physical and chemical properties of feed and stomach digesta

The particle size distributions of feed and digesta samples were characterised by the presence of three distinct peaks for all samples. As a representative example, particle size distributions of feed and stomach digesta from IB, GB and EB treatments are represented in Fig. 1. Diets with ground and extruded cereals consisted mainly out of medium-sized particles (71 vol% on average), whereas diets with isolated starch had a rather equal distribution of medium (42 vol% on average) and large particles

Table 3. Rheological properties of feed and digesta recovered from the stomach and two parts of the small intestine of pigs fed diets differing in starch source (barley, maize or high-amylose maize) and form (as isolated powder, ground cereal or extruded cereal)*†

		Experimental diets												
		Barley			Maize			High-amylose maize				*P*‡		
		Isolated	Ground	Extruded	Isolated	Ground	Extruded	Isolated	Ground	Extruded	Pooled SD	Form	Source	Form × source
Diet	Shear stress (Pa) at 1 Hz	147	238	445	202	213	344	166	152	196				
	Storage mod (Pa) at 1 Hz	1337	2067	4134	1853	1886	3045	1544	1371	1768				
	Loss mod (Pa) at 1 Hz	604	1180	1634	809	995	1601	603	664	838				
	tanδ	0·45	0·57	0·40	0·44	0·53	0·53	0·39	0·48	0·47				
Max obs§		10	10	9	10	10	9	7	7	10				
Stomach	Shear stress (Pa) at 1 Hz	590^{a,b}	620^{a}	20^{e}	550^{a,b,c}	460^{c}	0^{e}	570^{a,b,c}	480^{b,c}	200^{d}	84	<0·0001	0·020	<0·0001
	Storage mod (Pa) at 1 Hz	5194	5177	108	4933	4095	20	4993	4254	1840				
	Loss mod (Pa) at 1 Hz	2726	3242	49	2460	2016	9	2417	2000	751				
	tanδ	0·53^{b}	0·62^{a}	0·49^{b,c}	0·49^{b,c}	0·49^{b,c}	0·51^{b,c}	0·48^{b,c}	0·47^{c}	0·41^{d}	0·036	<0·0001	<0·0001	<0·0001
SI2	*K* (Pa × s)	98^{a,b,c}	85^{b,c}	62^{b,c}	118^{a,b}	64^{b,c}	34^{c}	132^{a,b}	167^{a}	62^{b,c}	39	<0·0001	0·001	0·012
	n	0·009	0·004	0·020	0·005	0·045	0·118	0·007	0·007	0·078	0·062	0·004	0·066	0·308
SI4	*K* (Pa × s)	251	110	142	210	137	158	220	216	120	75	0·001	0·708	0·083
	n	−0·001	0·002	0·001	0·000	0·000	0·000	0·011	−0·001	0·012	0·014	0·668	0·234	0·563

[a,b,c,d] When an interaction between form and source was found, unlike superscript letters indicate significant differences between dietary treatments ($P < 0·05$).

* Presented values for diet samples are averages of four measurements

† Presented values for digesta samples are estimated least-squares means and pooled standard deviations, except for the storage and loss moduli (mod), which are raw means.

‡ Model established *P*-values for fixed effects of starch form (isolated, ground and extruded), source (barley, maize and high-amylose maize), and the interaction between form and source, analysed per segment.

§ The maximum number of replicate observations (max obs) equals the number of replicate animals per dietary treatment. In some segments, not enough digesta was present to allow analyses, causing one missing observation in the stomach of pigs fed EM and SI2 of pigs fed GM, IA, GA and EA, two missing observations in SI2 of pigs fed EB and SI4 of pigs fed GM, EM and EA, three missing observations in SI2 of pigs fed IB and IM and SI4 of pigs fed GB and IM, and four missing observations in SI2 of pigs fed EM and SI4 of pigs fed IB and EB.

Table 4. Pearson correlation coefficients for digesta mean retention times (MRT) and rheological properties of diets, stomach and small intestinal (SI) digesta

	MRT_{solid} stomach	MRT_{liquid} stomach	MRT_{solid} SI2	MRT_{liquid} SI2	MRT_{solid} SI4	MRT_{liquid} SI4
Shear stress feed	−0·71*	−0·47	−0·22	−0·50	−0·05	−0·37
Shear stress stomach digesta	0·33***	0·19				
K SI2 digesta			0·02	0·07		
K SI4 digesta					0·02	0·09

* $P < 0·05$, *** $P < 0·001$.

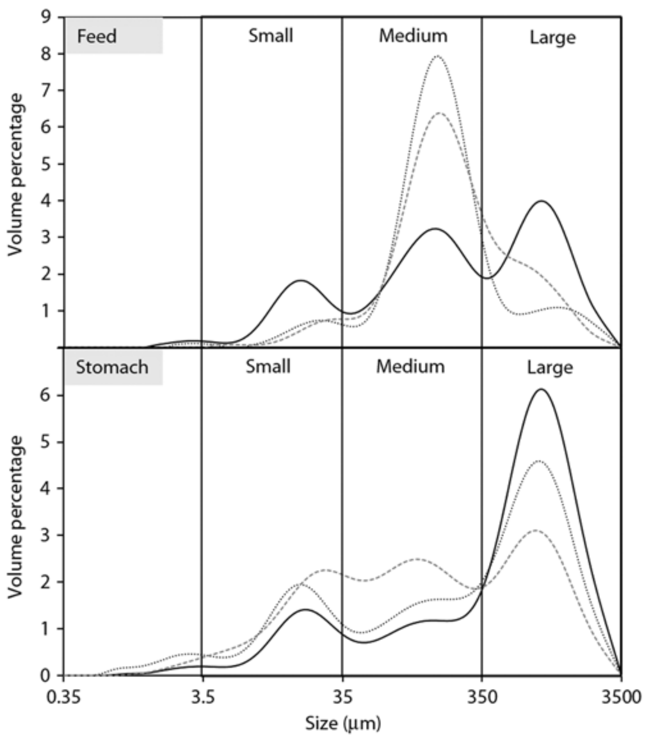

Fig. 1. Typical particle size distribution of barley-based diets, visualised for feed (top frame) and stomach digesta (bottom frame), which included isolated starch (solid line), ground cereals (dotted line) or extruded cereals (dashed line).

(40 vol% on average, Table 5). Stomach digesta consisted mainly of particles larger than 350 µm. As expected, the particle size fractions within diets and stomach digesta were highly correlated (Table 6). Dietary treatment effects on the particle size distribution of stomach digesta were therefore analysed for the large particle size fraction only. Stomach digesta of pigs fed ground diets contained more large particles (58 vol% on average) compared with that of pigs fed extruded diets (46 vol% on average), but less than pigs fed isolated diets (70 vol% on average, $P < 0·001$). Stomach digesta of pigs fed HA maize contained more large particles (63 vol% on average) than pigs fed barley (53 vol% on average, $P < 0·001$).

WHC (Table 5) of dry diets was comparable for diets containing isolated starch (2·2 ml/g) and ground cereals (1·9 ml/g). Extrusion increased the WHC with 2·1 ml/g for barley, 1·5 ml/g for maize and 0·6 ml/g for HA maize, compared with ground diets. Stomach digesta of pigs fed diets with isolated starch had a higher WHC (3·4 ml/g) than those of pigs fed ground and extruded diets (both 2·2 ml/g, $P < 0·001$).

Differences in stomach DM content were dominated by a higher digesta DM content for pigs fed ground diets compared with those fed isolated and extruded diets, particularly for barley and maize diets (form × source, $P < 0·001$, Table 5). The SR of diets was slightly above 1 for IB and IM, whereas it was below 1 for all other diets. The SR of stomach digesta obtained from pigs fed extruded cereals was higher than for pigs fed diets containing isolated starch or ground cereals, except for diets from HA maize origin (form × source, $P < 0·001$, Table 5). For diets from HA maize origin, the SR of stomach digesta from pigs fed extruded cereals was higher than for pigs fed diets with isolated starch, but not for pigs fed ground cereals (form × source, $P < 0·001$, Table 5).

Upon ingestion, the pH decreased on average with 2·6 unit points to 4·2 unit points (Table 5). Stomach pH was affected by an interaction between form and source of starch used. The pH of stomach digesta for pigs fed IA was lower than that of pigs fed GA (form × source, $P < 0·05$), whereas this difference was not observed for pigs fed barley or maize.

Soluble polymers in a water extract of feed and stomach digesta were analysed with HPSEC. A representative HPSEC profile is presented for maize starch in isolated, ground and extruded forms, in Fig. 2. Diets with extruded cereals had the highest concentration of large soluble polymers (molecular weight about 1000 kDa). Upon ingestion, the concentration of large polymers decreased, whereas an increase in small polymers (molecular weight about 1 kDa) was identified, especially for pigs fed extruded cereals. High-performance anion exchange chromatography (HPAEC) revealed the presence of maltodextrines DP 2–6 as typical breakdown products of starch (data not shown), accounting for 18 % of total starch in stomach digesta of pigs fed diets containing extruded cereals and for <5 % for pigs fed diets with ground cereals and isolated starch.

Correlations between rheological and physical properties of diets and stomach digesta

In the diets, shear stress was positively correlated with WHC (r 0·92, $P < 0·001$) and, consequently, negatively correlated with SR (r −0·91, $P < 0·001$, Table 6). In stomach digesta, shear stress correlated positively with the fraction of large particles (r 0·68, $P < 0·001$) and, consequently, negatively with the fraction of middle (r −0·71, $P < 0·001$) and small particles (r −0·53, $P < 0·001$). Additionally, in stomach digesta, shear stress was

Table 5. Physical properties of feed and digesta recovered from the stomach of pigs fed diets differing in starch source (barley, maize or high-amylose maize) and form (as isolated powder, ground cereal or extruded cereal)*†‡

	Experimental diets												
	Barley			Maize			High-amylose maize				*P*§		
	Isolated	Ground	Extruded	Isolated	Ground	Extruded	Isolated	Ground	Extruded	Pooled SD	Form	Source	Form × source
Feed													
PSD 3·5–35 μm (%)	17	6	5	14	6	10	19	6	4				
35–350 μm (%)	39	75	65	43	73	63	44	76	73				
350–3500 μm (%)	43	19	30	42	21	27	35	19	24				
WHC (ml/g)	2·1	2·1	4·2	2·1	1·9	3·4	2·4	1·9	2·5				
DM content (%)	91	91	96	90	91	96	90	91	96				
SR	1·11	0·85	0·51	1·11	0·94	0·63	0·97	0·94	0·85				
pH	6·6	7·0	7·0	6·7	6·9	6·9	6·6	6·8	6·9				
Stomach digesta													
Max obs‖	10	10	9	10	10	9	7	7	10				
PSD 3·5–35 μm (%)	13	20	23	13	12	19	13	12	18				
35–350 μm (%)	16	25	38	16	29	33	15	2	25				
350–3500 μm (%)	$70^{k,y}$	$52^{l,y}$	$37^{m,y}$	$70^{k,x,y}$	$58^{l,x,y}$	$47^{m,x,y}$	$70^{k,x}$	$65^{l,x}$	$55^{m,x}$	4·5	<0·0001	<0·001	0·074
WHC (ml/g DM)	$3·3^{k}$	$2·3^{l}$	$2·2^{l}$	$3·2^{k}$	$2·2^{l}$	$2·3^{l}$	$3·5^{k}$	$2·0^{l}$	$2·1^{l}$	0·3	<0·0001	0·812	0·248
DM content (%)	$23^{c,d}$	32^{a}	$22^{c,d}$	25^{c}	35^{a}	21^{d}	$24^{c,d}$	33^{a}	29^{b}	2·3	<0·0001	<0·001	<0·0001
SR	$1·02^{b,c}$	$0·93^{c}$	$1·66^{a}$	$1·00^{b,c}$	$0·90^{c}$	$1·73^{a}$	$0·92^{c}$	$0·98^{b,c}$	$1·23^{b}$	0·19	<0·0001	0·003	<0·001
pH	$4·3^{a,b}$	$4·1^{a,b}$	$4·6^{a}$	$4·0^{a,b}$	$4·3^{a,b}$	$3·9^{a,b}$	$3·6^{b}$	$4·7^{a}$	$4·2^{a,b}$	0·5	0·047	0·178	0·008

a,b,c,d When an interaction between form and source was found, unlike superscript letters indicate significant differences between dietary treatments ($P < 0·05$).
k,l,m In the absence of source × form interactions, unlike superscript letters are used to indicate significant differences between starch forms ($P < 0·05$).
x,y In the absence of source × form interactions, unlike superscript letters indicate significant differences between starch sources ($P < 0·05$).
* Presented values for diet samples are averages of duplicate measurements.
† Presented values for digesta samples are estimated least-squares means and pooled standard deviations.
‡ Abbreviations used for physical properties: particle size distribution (PSD), water-holding capacity (WHC) and saturation ratio (SR).
§ Model established *P*-values for fixed effects of starch form (isolated, ground and extruded), source (barley, maize and high-amylose maize) and the interaction between form and source, analysed per segment.
‖ The maximum number of replicate observations (obs) equals the number of replicate animals per dietary treatment. For WHC, DM and pH, the actual number of observations equals the maximum number of observations. For some animals, not enough digesta was collected and stored fresh to allow particle size analysis, causing one missing observation in pigs fed EB, IM, GM, IA, GA and EA, two missing observations in pigs fed GB, three missing observations in pigs fed IB and four missing observations in pigs fed EM.

Table 6. Pearson correlation coefficients for rheological and physical properties of diets and stomach digesta and mean retention times (MRT) of stomach digesta

	Vol% large particles	Vol% middle particles	Vol% small particles	DM	WHC	SR	pH	Stomach MRT_{solid}	Stomach MRT_{liquid}
Diets									
Shear stress	−0·13	0·23	−0·38	0·78*	0·92***	−0·91**	0·66	−0·71*	−0·47
Vol% large particles		−0·97***	−0·81**	−0·03	0·06	0·42	−0·74*	−0·21	0·28
Vol% middle particles			−0·93***	−0·17	0·05	−0·50	−0·83**	0·15	−0·34
Vol% small particles				−0·35	−0·21	0·56	0·90***	0·03	0·39
DM					0·87**	−0·79*	0·50	−0·76*	−0·59
WHC						−0·88**	0·44	−0·85**	−0·48
SR							−0·76*	0·69*	0·60
Stomach digesta									
Shear stress	0·68***	−0·71***	−0·53***	0·40***	0·41***	−0·76***	−0·14	0·33***	0·19
Vol% large particles		−0·92***	−0·88***	0·13	0·51***	−0·58***	−0·26*	0·17	0·17
Vol% middle particles			0·64***	−0·05	−0·56***	0·56***	0·30*	−0·12	−0·12
Vol% small particles				−0·25*	−0·32**	0·53***	0·16	−0·22	−0·19
DM					−0·37**	−0·61***	0·14	0·37***	0·20
WHC						−0·48***	−0·20	0·17	0·15
SR							0·05	−0·48***	−0·29**

WHC, water-holding capacity; SR, saturation ratio.
* $P<0·05$, ** $P<0·01$, *** $P<0·001$.

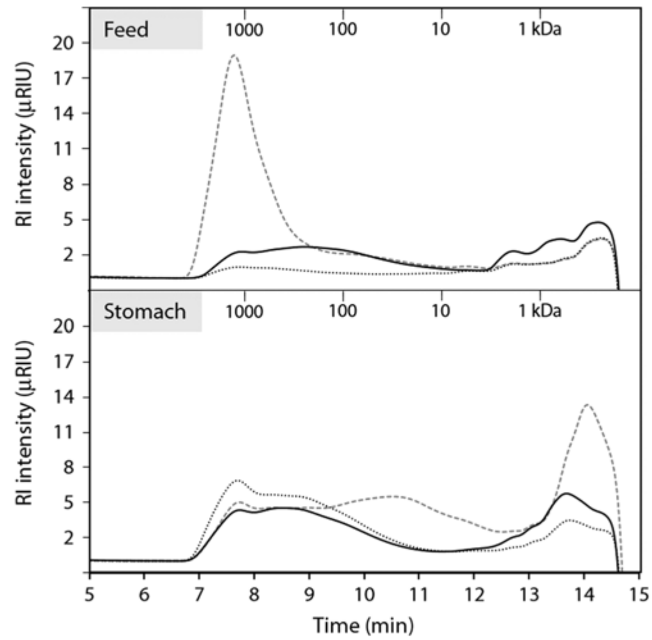

Fig. 2. Soluble polysaccharide profile of maize-based diets, which included isolated starch (solid line), ground cereals (dotted line) or extruded cereals (dashed line), visualised for feed (top frame) and stomach digesta (bottom frame), as measured with high-performance size exclusion chromatography. The second x-axis indicates the molecular weight calibration curve for pullulan. RI, refractive index; RIU, refractive index unit.

positively correlated with WHC (r 0·41, $P<0·001$) and negatively with SR (r −0·76, $P<0·001$).

In both diets and stomach digesta, WHC was negatively correlated with the SR, of which the correlation was stronger for diets (r −0·88, $P<0·001$) compared with stomach digesta (r −0·48, $P<0·0001$). All three volume fractions of particles in the diets correlated with the pH, but none with the WHC. For the diets, the strongest correlation was identified between the volume percentage of small particles and pH (r 0·90, $P=0·001$). In stomach digesta, all three volume fractions of particles correlated with the WHC, of which the correlation with middle-sized particles was strongest (r −0·56, $P<0·001$). All three volume fractions of particles also correlated with the SR, of which the correlation with large particles was strongest (r −0·58, $P<0·001$). The pH positively correlated with large (r 0·26, $P<0·05$) and middle-sized particles (r 0·30, $P<0·05$) and small particles negatively correlated with DM content (r −0·25, $P<0·05$).

Correlations between digesta mean retention time and physical properties of diets and stomach digesta

Solid digesta MRT in the stomach of pigs was negatively correlated with the WHC (r −0·85, $P<0·01$) and the DM content of the fed diets (r −0·76, $P<0·05$, Table 6). In addition, solid digesta MRT in the stomach was positively correlated with the SR (r 0·69, $P<0·05$). In the stomach, the SR of digesta was negatively correlated with both solid digesta MRT (r −0·48, $P<0·001$) and liquid digesta MRT (r −0·29, $P<0·01$). Solid digesta MRT was positively correlated with the digesta DM content (r 0·37, $P<0·01$).

Discussion

With the present study, we aimed to elucidate the role of digesta rheology in digesta transport through the upper GIT for pigs fed diets widely varying in physical and chemical properties. To this end, we designed nine dietary treatments with varying forms and sources of starch and measured digesta transport and digesta rheology as well as underlying physical and chemical digesta properties.

Effect of variation in starch form and source on digesta mean retention time in the upper gastrointestinal tract

Solid fractions of digesta needed on average 4·9 h to pass the stomach and SI of young growing pigs, which is in line with previous research[10,11,39,40]. The effects of digesta passage behaviour on nutrient absorption kinetics were dominated by stomach MRT, as digesta MRT in the stomach was longer than that of the SI, which corresponds to previous research[11]. As expected[10,11], we found that the passage rate for the liquid digesta fraction typically exceeded that of solids in the stomach, but not necessarily in the SI.

Our findings indicate that the largest dietary treatment effects on solid digesta MRT were caused by extrusion, which reduced the digesta MRT in the stomach compared with ground cereals. In addition, EB tended to remain shorter in the SI compared with GB. The reduction in digesta MRT in the pig's stomach, caused by processing, is in line with previous research, which reported that a hydrothermal treatment of a maize-based diet decreased the total dry mass in the stomach of pigs[41]. Replacing native starch with gelatinised starch, however, did not decrease gastric retention times in pigs[42], which suggests that the reduction in gastric retention time, caused by extrusion, is related to other feed traits than starch gelatinisation.

No differences in MRT of solid digesta in the upper GIT of pigs fed IA and IM were found. This supports previous findings on the glycaemic response of starch that differed in amylose content: In this previous study, a similar gastric emptying rate was assumed for both low and HA diets, which resulted in a strong relation between the *in vitro* digestibility rate and the time of portal glucose appearance *in vivo*[43].

In our study, we observed a longer MRT of solid digesta in the SI of pigs fed IB compared with pigs fed GB. Numerically, the difference in MRT is largest in SI3 (Table 1), where the digestion coefficient of starch originating from GB (0·87) was lower than that of IB (0·96)[26]. Consequently, the longer MRT of IB seems to be caused by other components in the feed matrix than starch, which were mainly soyabean meal and soyabean hulls in the IB diet. This corresponds well with the reduction in MRT of SI digesta found when replacing soyabean with cereal-based material[40], as GB contains more cereal-based material compared with IB.

Rheological characterisation of diets and digesta

The rheological behaviour of feed and stomach digesta was characterised by their complex moduli, where the storage modulus (G′) indicates elastic, solid-like behaviour and the loss modulus (G″) indicates viscous, fluid-like behaviour[44]. For all experimental diets, G′ exceeded G″ and thus tanδ was below 1, which indicates that diets behaved as a weak gel[31,45]. Based on the shear stress, we concluded that isolated and ground diets were easiest to deform. In the present study, we did not carry out an amplitude sweep prior to the oscillatory frequency sweep. Consequently, we cannot be sure that the frequency sweep was performed in the linear viscoelastic range. Hence, we should take care in the interpretation of the shear stress, which summarises the rheological characteristics of diets and digesta, but can reflect both reversible and irreversible viscoelastic behaviour in the present study[37].

For all dietary treatments, stomach digesta was characterised as a weak gel, as found previously for stomach digesta of pigs[46]. The low shear stress observed for stomach digesta of pigs fed extruded diets corresponds well with the previous research, which reported a higher fluidity of stomach digesta for pigs fed hydrothermal treated diets compared with non-hydrothermal treated diets[41]. In our study, shear stress of stomach digesta of pigs fed ground cereals depended on the source of starch included, resulting in a lower digesta shear stress for pigs fed GB, compared with GM and GA.

Upon transport of digesta from the stomach to the SI, the fluidity of digesta increased and rheology measurements as performed for stomach digesta were not possible. The increase in fluidity after passage of the stomach is likely related to the lower DM content in the SI compared with the stomach (on average 13 %, data not shown). It is well known that solids are retained longer in the porcine stomach than liquids[10,11], which is consistent with the difference in MRT between stomach liquids and solids, observed in our study. Usually, large particles (diameter > 1–2 mm) remain in the human stomach until the particle size is reduced sufficiently[16,18]. The accumulation of large particles in the porcine stomach will likely have caused SI digesta to consist mainly out of small particles. The apparent viscosity of composite suspensions such as digesta depends highly on the ratio between the volume fraction of particles and the maximum packing fraction[9]. Due to the lower DM content and smaller, more homogeneous, size of particles in SI digesta, particles present in SI digesta will contribute less to the whole digesta rheology, compared with stomach digesta[12].

Relation between digesta properties and gastric mean retention time

Confirming our hypothesis, the MRT of digesta in the stomach of pigs can be partly explained by the shear stress of digesta (Table 6). The shear stress is related to all underlying physical properties measured but, surprisingly, does not necessary explain a larger part of variation in MRT than these underlying properties. Especially, the SR explains a large fraction of variation in stomach MRT for both solid and liquid fractions of digesta (Table 6). The SR indicates the digesta water content, as fraction of the theoretical maximum of water that can be held by the DM according to its WHC. In addition to the WHC of digesta, the SR is strongly affected by the total dry mass in the stomach. The total dry mass, in turn, is affected by properties of the insoluble particulate fraction. In the case of liquids, the negative relation between MRT and SR indicates that water held

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in the digesta matrix is emptied slower from the stomach than free water. This relation appears more complex in the case of solids, as the behaviour of the solid fraction of digesta depends greatly on the properties of the particulate matter. Compared with the diets with ground and extruded cereals, the diets with isolated starch were richer in soyabean hulls, soyabean meal and sugar beet pulp[26]. These ingredients generally have higher WHC than maize and barley meals[47]. Based on this higher WHC, we expected a lower SR for stomach digesta of pigs fed diets with isolated starch compared with diets that included ground cereals. The SR of stomach digesta, however, did not differ between diets with isolated starch and diets with ground cereals (Table 5). To further unravel the relation between the SR and MRT of stomach digesta, we studied Pearson correlation coefficients for digesta properties and MRT after omitting diets with one starch form at a time (data not shown). When omitting diets with ground cereals from the data set, we observed an increase in the relation between digesta WHC and SR (r −0·75, $P < 0{\cdot}001$) whilst the relation between digesta SR and MRT of solids remained rather constant (r −0·46, $P < 0{\cdot}001$). This indicates that the decreased SR of digesta of pigs fed diets with isolated cereals, compared with pigs fed extruded cereals, is dominated by the WHC of digesta. In contrast, omitting diets with isolated starch from the dataset resulted in a stronger relation between digesta DM and SR (−0·92, $P < 0{\cdot}001$), but again not in differences in the relation between digesta SR and MRT of solids (r −0·54, $P < 0{\cdot}001$). This indicates that the decreased SR of digesta of pigs fed diets with ground cereals, compared with pigs fed extruded cereals, is dominated by the DM content. The DM content in the stomach of pigs fed ground cereals was higher than that of pigs fed diets with isolated starch, whereas the total weight of stomach digesta did not differ between those dietary treatments ($P > 0{\cdot}1$, data not shown). It seems that more solid particles accumulate in the stomach of pigs fed ground cereals, than in those of pigs fed diets with isolated starch. In conclusion, a considerable part of the variation in gastric MRT can be explained by the SR of digesta, which appears to depend greatly on the physical properties of the particulate matter in the stomach.

Predicting gastric mean retention times with dietary characteristics

In contrast to the negative correlation between digesta SR and MRT of solids in the stomach of pigs, dietary SR correlated positively with MRT. Dietary WHC was especially high, causing a low dietary SR, in diets containing extruded cereals, particularly barley and maize. This increase in WHC is caused by starch gelatinisation during extrusion, which greatly increases the WHC of starch[48–50]. HA maize starch has, due to its molecular properties, a higher gelatinisation temperature, which results in a lower degree of gelatinisation compared with barley and maize when extruded under similar conditions[49,51,52]. The physiological function of the stomach, however, causes several changes in physical and chemical properties of diets compared with digesta. This led to different relations between (1) WHC and SR and (2) properties of the particulate fraction and SR, for diets and stomach digesta. Firstly, the strong correlation observed between dietary WHC and SR was much lower for stomach digesta. Using chromatographic analysis, we observed breakdown products of starch upon ingestion, predominantly in extruded diets. Breakdown of the starchy network may explain the decrease in WHC from diets to digesta, and consequently the increase in SR. This fits well with the previous research reporting a higher fluidity of stomach digesta in pigs fed hydrothermal processed diets compared with pigs fed unprocessed diets[41]. Starch breakdown in the stomach may also explain earlier observations of a starch-induced increase in dietary WHC, which led, unexpectedly, not to an increased stomach MRT of solids[42]. Secondly, the volume percentage of large particles in the stomach correlated negatively with SR, whereas this correlation was absent in the diets. Large particles constituted a greater volume fraction of stomach digesta than in the diets, which complicates the prediction of the contribution of the particulate matter to whole digesta properties and rheology. In turn, both the accumulation of large particles and the decrease in WHC during retention in the stomach hinder predictability of gastric retention times based on feed properties.

Conclusions

The greatest effects of dietary treatments on solid digesta MRT of pigs fed starch rich diets were observed in the stomach, where extrusion reduced MRT of solids by 29–75 min. Rheological analysis of whole digesta revealed that gastric digesta behaved as a gel-like material. Variations in digesta shear stress explained part of the variation in solid stomach digesta MRT, but not in liquid digesta MRT. Relationships among rheological properties and small intestinal MRT were absent. Unexpectedly, not shear stress, but the SR explained most variation in stomach MRT of both solids and liquids: An increased SR related to a decreased MRT. The low SR of extruded diets, related to the high WHC of gelatinised starch, increased considerably after ingestion. Large particles accumulated in the stomach of pigs and correlated negatively with the SR of stomach digesta, but not with that of diets. Due to these changes in chemical and physical properties upon ingestion, the MRT of stomach digesta cannot be easily predicted from dietary properties.

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the manuscript. All authors have read and approved the final manuscript.

B. M. J. M. and E. M. A. M. B. are employees of the Royal Agrifirm Group. All other authors declare that they have no conflicts of interest.

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