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Increased diet viscosity by oat β-glucans decreases the passage rate of liquids in the stomach and affects digesta physicochemical properties in growing pigs

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*Rheological properties of digesta play a role in digesta passage kinetics through the gastrointestinal tract, in turn affecting nutrient absorption kinetics. Therefore, we studied the effects of diet viscosity on digesta passage and physicochemical properties in pigs. Twenty male growing pigs (35 kg body weight at the start) were assigned to one of five diets with increasing dietary concentrations of β-glucans (**BG**; from 0 % to 10 %), in exchange for maize starch. After a 17-day adaptation period, pigs were euthanised and the mean retention time (**MRT**) of digesta solids (TiO_2) and liquids (Cr-EDTA) in the stomach, and proximal and distal half of the small intestine was quantified. In the stomach, the MRT of liquids, but not of solids, increased when dietary BG level increased (6 min per % dietary BG,* $P = 0.008$ *and* $R^2 = 0.35$*). Concomitantly, stomach DM content (5 g/kg per % dietary BG,* $P < 0.001$ *and* $R^2 = 0.53$*) and apparent digesta viscosity (56 Pa × s at 1/s shear rate per % dietary BG,* $P = 0.003$ *and* $R^2 = 0.41$*) decreased. In the proximal half of the small intestine, no effects of dietary BG level were observed. In the distal half of the small intestine, water-binding capacity (**WBC**) of digesta increased (0.11 g/g digesta DM per % dietary BG,* $P = 0.028$ *and* $R^2 = 0.24$*) and starch digestibility decreased (0.3% per % dietary BG,* $P = 0.034$ *and* $R^2 = 0.23$*) when dietary BG level increased. In the colon, apparent digesta viscosity at 45/s shear rate increased (0.1 Pa × s per % dietary BG,* $P = 0.03$ *and* $R^2 = 0.24$*) in the proximal half of the colon, and digesta WBC increased (0.06 g/g digesta DM per % dietary BG,* $P = 0.024$ *and* $R^2 = 0.26$*) in the distal half of the colon when dietary BG level increased. To conclude, increasing dietary BG level caused the MRT of liquids, but not that of solids, to increase in the stomach, resulting in reduced separation of the solid and liquid digesta fractions. This caused dilution of the stomach content and reduction in digesta viscosity when dietary BG levels increased. Effects of dietary BG level on physicochemical properties in the proximal small intestine were absent and may have been due to a low DM content. The WBC of digesta in the distal small intestine and colon increased when dietary BG level increased, as did apparent digesta viscosity in the proximal colon. This likely reflects the concentration of BG in digesta when moving through the gastrointestinal tract.*

Keywords: digesta mean retention time, gastrointestinal tract, solids, rheology, digestion kinetics

Implications

This study quantifies the relation between diet viscosity, induced by dietary β-glucans, digesta apparent viscosity and passage kinetics of liquid and solid digesta fractions in the gastrointestinal tract. The difference between passage of digesta solids and liquids decreased with increasing diet viscosity. These results can be used to improve predictions of nutrient absorption kinetics, by using, for example, mechanistic digestion simulation models. Increased understanding of kinetics of the digestive process and absorption of nutrients will facilitate optimising diet formulation strategies to increase efficient metabolic use of nutrients, by taking into account variation in digestion kinetics among feed ingredients and diets.

Introduction

Currently, the nutritional value of feed ingredients for pigs is based on ileal or total tract nutrient disappearance. Feeding tables, containing (standardised) ileal digestibility values for amino acids per feed ingredient (e.g. L'Institut national de la recherche agronomique, 2004; Centraal Veevoeder Bureau, 2012; National Research Council, 2012), are of great importance to formulate diets that meet the pigs' requirement for essential amino acids. However, it was shown that the

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metabolic fate of absorbed nutrients can be influenced by differences in portal appearance kinetics between nutrients (Batterham and Bayley, 1989; van den Borne *et al*., 2007).

Portal appearance kinetics of glucose and amino acids depend on the kinetics of feed intake, digesta passage and nutrient hydrolysis and absorption. As the small intestine is the major site of nutrient absorption, digesta passage in proximal segments of the gastrointestinal tract (**GIT**), especially the stomach, dominates portal nutrient appearance. In turn, dietary fibres can influence digesta passage kinetics (Rainbird and Low, 1986a and 1986b; Johansen *et al*., 1996), depending on, among others, their capacity to affect digesta viscosity (Cherbut *et al*., 1990; Marciani *et al*., 2001). The latter can be dependent on dietary fibre concentration (Rainbird and Low, 1986a), fibre physical and chemical properties (Owusu-Asiedu *et al*., 2006; Hooda *et al*., 2011) and location in the GIT (Potkins *et al*., 1991; Owusu-Asiedu *et al*., 2006). Hence, the current study aimed to evaluate the relation between diet viscosity, digesta passage and digesta physicochemical properties in various locations of the GIT in growing pigs. We hypothesised that an increase in diet viscosity would increase digesta viscosity in the stomach and small intestine, thereby increasing the mean retention time (**MRT**) of digesta in these segments.

Material and methods

The study was approved by the Dutch Animal Ethics Committee (2014.III.06.056) and carried out at the Swine Research Centre of Nutreco N.V. (Sint Anthonis, the Netherlands).

Animals and housing

Twenty male growing pigs (Hypor × Maxter; Hendrix Genetics, Boxmeer, the Netherlands) with an average initial BW of 34.6 ± 1.4 kg were used. Pigs were individually housed in pens (2.48 × 0.94 m) equipped with partial slatted floors and half-open walls between pens to allow visual and physical contact of adjacently housed pigs. Temperature was controlled at 23°C ± 1°C, and facilities were lit from 0600 to 1800 h. Feeding schedule, sample collection and chemical analysis were executed as previously described by Schop *et al.* (2019).

Diets and feeding

Pigs were assigned to one of five experimental dietary treatments. Dietary treatments consisted of five incremental levels of dietary β-glucans (**BG**): 0%, 2.5%, 5%, 7.5% and 10%, referred to as BG0, BG2.5, BG5, BG7.5 and BG10 (Table 1). The diets were obtained by mixing different ratios of the BG0 and BG10 diet. These two diets were formulated by exchanging maize starch in the BG0 diet, for a BG extract (PromOat, Tate & Lyle PLC, London, UK) in the BG10 diet, while maintaining equal levels of digestible nutrients and energy (Table 2). Diets were formulated to meet or exceed nutrient requirements for growing pigs according to CVB (2012). The feeds were produced as a mash. Soybean meal, maize and wheat were hammer-milled using a 4-mm sieve, and rapeseed meal and sugar beet pulp using a 2.75-mm sieve.

Table 1 *Dietary treatments consisting of five incremental levels of β-glucans (BG) (0%, 2.5%, 5%, 7.5% and 10%) resulting from mixing of the control (BG0) and 10% β-glucans (BG10) diets, including apparent dynamic viscosity properties[1] of the five diets, fed to growing pigs*

Dietary treatments[2]	BG0	BG10	*K* (SD) Pa × s	*n* (SD)	Visco45 (SD) Pa × s
BG0	100	0	39 (4.6)	−0.50 (0.517)	0.38 (4.4)
BG2.5	75	25	30 (9.8)	0.50 (0.0215)	4.4 (1.11)
BG5	50	50	117 (16.8)	0.29 (0.0437)	7.8 (0.26)
BG7.5	25	75	315 (46.5)	−0.13 (0.0170)	4.3 (0.36)
BG10	0	100	581 (97.6)	−0.27 (0.175)	5.1 (2.90)

[1] Derived from dynamic viscosity by using a power-law function: $= K\dot{\gamma}^{n-1}$, where η = viscosity (Pa × s), $\dot{\gamma}$ = shear rate (/s), n = power law index, K = consistency constant (Pa × s) and visco45 = apparent viscosity at $\dot{\gamma} = 45$/s (Pa × s).

[2] Number of observations was two per diet, except for BG5 and BG10 where the number of observations was three.

Three days prior to the experiment, the pigs were gradually switched from the commercial diet to the experimental diets. The experiment lasted for 18 days. Pigs were fed the experimental diets at a daily feeding level of three times their metabolisable energy requirement for maintenance (419 kJ /kg $BW^{0.75}$; Centraal Veevoeder Bureau, 2005). The pigs were fed twice daily at 0800 and 1600 h until day 15, followed by frequent feeding from day 16 onwards to induce steady-state passage of digesta in the GIT. During the frequent feeding period, daily feed allowance was divided in six equal portions. On days 16 and 17 pigs received portions once every 3 h from 0530 until 2030 h. On day 18 pigs received portions once every 2 h from 0230 h until 2 h prior to euthanasia, with a minimum of three portions fed on this day. Feeding time on day 18 was scheduled according to the pre-planned time of euthanasia of each pig, starting at 0830 h. The diets contained TiO_2 (4.0 g/kg diet) as the indigestible insoluble marker (Jagger *et al*., 1992) from day 8 onwards, and Cr-EDTA (1.9 g/kg diet) as the indigestible soluble marker (Udén *et al*., 1980) from day 11 onwards. Diets were fed as mash and mixed with water (1:2.5, wt: wt) in the feed trough. In addition, pigs received 0.5 l of water per day, 0.25 l in the morning and 0.25 l in the afternoon. During frequent feeding, pigs did not receive additional water. Pigs were weighed twice weekly to adjust the feed allowance to the pigs' BW.

Sample collection and chemical analysis

At day 18 the pigs (48.9 ± 2.3 kg BW) were euthanised for quantitative digesta collection from the stomach, proximal and distal half of the small intestine based on length (further mentioned as proximal or distal small intestine, respectively), caecum, and proximal and distal half of the colon based on length (further mentioned as proximal or distal colon,

Table 2 *Ingredient and chemical composition of the control (BG0) and 10% β-glucans (BG10) diet fed to growing pigs*

Ingredients (g/kg)	BG0	BG10
Maize starch (native)	232.3	0.0
PromOat Beta Glucan[1]	0.0	299.2
Sucrose	17.0	0.0
Oat hulls	48.7	0.0
Soy oil	20.8	10.4
Wheat gluten meal	18.1	9.1
Water	0.0	18.3
Wheat	200.0	
Soybean meal	139.9	
Maize	104.8	
Wheat middlings	100.0	
Rapeseed meal	80.0	
$CaCO_3$	11.3	
Monocalcium phosphate	7.0	
Premix[2]	5.0	
L-Lysine	3.5	
NaCl	2.5	
$Na(CO_3)_2$	1.3	
L-Threonine	0.9	
DL-Methionine	0.8	
L-Tryptophan	0.2	
TiO_2	4.0	
Cr-EDTA	1.9	
Analysed chemical composition (g/kg as-is)[3]		
DM	887	887
Crude ash	57	63
CP	162	164
Crude fat	38	41
Starch	404	303
Reducing sugars	54	65
NSP[4]	173	254
ME[5], MJ/kg as-is	13.3	13.3

[1] PromOat Beta Glucan, Tate & Lyle PLC, London, UK. β-glucan content 35%. Analysed content, g/kg of product: 45 DM, 22 ash, 42 CP, 46 crude fat, 326 starch, 63 reducing sugars.

[2] Premix composition, /kg diet: 8000 IU vitamin A, 1600 IU vitamin D_3, 30 mg vitamin E, 1.5 mg vitamin K_3, 1.0 mg vitamin B_1, 4.0 mg vitamin B_2, 1.5 mg vitamin B_6, 20 µg vitamin B_{12}, 20 mg niacin, 12 mg D-pantothenic acid, 150 mg choline chloride, 0.2 mg folic acid, 100 mg Fe (as $FeSO_4.H_2O$), 20 mg Cu (as $CuSO_4.5H_2O$), 30 mg Mn (as MnO), 70 mg Zn (as $ZnSO_4.H_2O$), 0.68 mg I (as KI), 0.20 mg Se (as Na_2SeO_3). Carrier: maize meal.

[3] Chemical composition presented as g/kg as-is, unless stated otherwise.

[4] Non-starch polysaccharides as calculated from calculated diet composition: organic matter – CP – crude fat – starch – gluco-oligosaccharides – 0.9 × sugar (CVB, 2012).

[5] Metabolisable energy (MJ) = (20.0 × digestible CP + 39.1 × digestible ether extract + 17.5 × starch + 16.6 × sugars + 17.2 × digestible NSP)/1000 (Noblet *et al.*, 1994).

respectively). After digesta collection, digesta samples were cooled and stored at 4°C pending analyses for dynamic viscosity (analysed within 96 h) and water-binding capacity (**WBC**; analysed within 24 h), while remaining digesta were stored at −80°C and freeze-dried before analyses for chemical content (DM (ISO 6496:1999), CP (N × 6.25, ISO 5983:2005), starch (ISO 15914:2004), reducing sugars (van Vuuren *et al.*, 1993), titanium (Myers *et al.*, 2004) and chromium (van Bussel *et al.*, 2010) after sample preparation by (Williams *et al.*, 1962)).

Water-binding capacity of digesta was measured using centrifugal force. Fresh digesta samples were centrifuged at 4000 × **g** for 10 min at 21°C after which the supernatant was decanted. The WBC, in g/g digesta DM, was calculated as the weighed amount of water retained after decanting. This analysis was performed in duplicate if the quantity of available sample allowed. In total there were 12 missing observations: 9 in the proximal small intestine, 2 in caecum, 1 in the proximal colon.

Dynamic viscosity of solutions can be quantified by measuring the force (i.e. stress) needed to make a sample flow at (various) rates. Considering the non-Newtonian, shear-thinning, behaviour of digesta and effects of particles on digesta flow behaviour (Shelat *et al.*, 2015), the apparent dynamic viscosity of digesta and diets was measured by applying a continuous shear rate sweep. Dynamic viscosity of digesta was measured within 96 h after digesta collection by an MCR502 and MCR301 rheometer (Modular Compact Rheometer, Anton Paar GmbH, Graz, Styria, Austria). Measurements were carried out at 39°C with declining shear rates from 50/s to 1/s in 25 steps after a 30 s pre-shear at 10/s. Due to variation in digesta consistency among GIT segments, different geometries were used. Stomach and small intestinal digesta samples were measured in a titanium concentric cylinder (i.e. cup) system (CC17-SN2540, Anton Paar GmbH, Graz, Austria). Caecal and colon digesta samples were measured on a titanium parallel profiled plate-plate measuring system (PP25/P2-SN25463; PP25/P2-SN25491, Anton Paar GmbH, Graz, Austria) with a 1.5-mm gap width. The latter geometry was also used to measure dynamic diet viscosity of as-fed diet samples (diet to water ratio 1 : 2.5, wt : wt). Measurements were carried out as for digesta samples, with the exception that temperature was 24°C.

Calculations and statistics

Calculations and statistical analyses were performed in SAS version 9.3 (SAS Institute Inc., Cary, NC, US). The retention time of digesta, being inversely related to the fractional passage rate, was studied in the stomach, and proximal and distal small intestine. The retention time was calculated (equation 1) and further defined as the MRT of digesta in each segment. Based on the assumption that in a steady state, pool sizes of indigestible marker in each segment reflect the MRT of digesta in that segment (de Vries and Gerrits, 2018):

$$\text{MRT}\,(\text{min}) = \frac{\text{Marker pool size in digesta}\,(g)}{\text{Marker intake}\,\left(\frac{g}{h}\right)} \times 60 \quad (1)$$

where marker is either Ti (as TiO_2) or Cr (as Cr-EDTA), marker pool sizes in digesta were calculated for each GIT segment by multiplying the digesta marker concentration (g/kg DM) by the weight of digesta in the corresponding segment (g DM). Marker intake was calculated by multiplying

diet marker concentration (g/kg DM) with hourly feed intake (g DM) during bi-hourly feeding.

Apparent digestibility of starch and protein in the stomach, proximal and distal small intestine was calculated (equation 2) according to Kotb and Luckey (1972):

$$\text{Nutrient digestibility}\,(\%) = \left(1 - \frac{\left(\frac{[\text{Nutrient}]_{\text{digesta}}}{[\text{Marker}]_{\text{digesta}}}\right)}{\left(\frac{[\text{Nutrient}]_{\text{diet}}}{[\text{Marker}]_{\text{diet}}}\right)}\right) \times 100 \quad (2)$$

where $[\text{Nutrient}]_{\text{digesta}}$, $[\text{Nutrient}]_{\text{diet}}$, $[\text{Marker}]_{\text{digesta}}$, $[\text{Marker}]_{\text{diet}}$ are concentrations (g/kg DM) of nutrient (CP or starch) and marker (Ti) in the digesta or diet samples.

Dynamic digesta viscosity is described to have non-Newtonian shear-thinning flow behaviour. Therefore, the non-Newtonian flow behaviour was fitted using a power-law model (equation 3; Shelat *et al.*, 2015):

$$\eta = K\,\dot{\gamma}^{n-1} \quad (3)$$

where η = apparent shear viscosity (Pa × s), K = consistency constant, $\dot{\gamma}$ = shear rate (/s) and n = power-law index. The power-law model parameters (K, n) were estimated per pig per GIT segment using non-linear least squares regression (PROC NLIN). In addition, apparent viscosity at 45/s (Newtonian region) was calculated from the power-law model and reported.

The effects of dietary BG level on digesta MRT, nutrient digestibility and digesta physicochemical properties were analysed per GIT segment using regression analysis (PROC REG) and dietary BG concentration as regressor. Pig was considered as the experimental unit. In addition, regression analysis was performed on dynamic diet viscosity parameters and dietary BG level (regressor). Linear and quadratic regressions were performed. Model residuals were tested for normality using the Shapiro–Wilk Test, and visually evaluated to confirm heteroscedasticity. Results are presented as intercept, slope, pooled SEM, model established P-values and R^2 representing the goodness of fit. A Pearson's correlation matrix (PROC CORR) was established for digesta physicochemical properties per GIT segment, whereby observations of the proximal and distal halves of the intestines were combined for the small intestine and colon, respectively. Differences were considered significant at $P < 0.05$ and a trend at $P < 0.1$.

Results

All pigs remained clinically healthy during the study. All meals were finished within 15 min by the pigs. The results for the stomach segment of one pig were considered as outlier (MRT: 6.2 h, exceeded the overall mean + 2 × SD and was marked as outlier using Cook's D) and were excluded from further statistical analyses. An overview of mean and SD of all analysed parameters (i.e. MRT, nutrient digestibility, physicochemical properties) per dietary treatment is provided as supplementary tables (Supplementary Tables S1, S2 and S3, respectively).

Dietary BG level appeared positively correlated with consistency constant K (36.9 − 20.8 × dietary BG (%) + 7.6 × dietary BG (%)^2, P quadratic term = 0.002, $R^2 = 0.99$, RMSE = 7.8) and apparent viscosity at 45/s shear rate (2.5 + 0.38 × dietary BG (%), $P = 0.015$ and $R^2 = 0.31$) of the diet (data not presented).

Mean retention time

On average (mean ± SD), over all dietary treatments, the MRT of solids and liquids was 122 (±38) and 69 (±34) min (stomach), 21(±9) and 21(±10) min (proximal small intestine) and 89(±25) and 100(±26) min (distal small intestine). Stomach MRT of liquids significantly increased when dietary BG level increased (6 min per % dietary BG, $P = 0.008$ and $R^2 = 0.35$; Table 3), thereby reducing the difference between stomach MRT of solids and liquids (6 min per % dietary BG, $P < 0.0001$ and $R^2 = 0.63$). No effects on the MRT of solids and liquids were observed in the proximal and distal small intestine.

Digestibility

On average (mean ± SD), over all dietary treatments, apparent digestibility of starch and protein was 96% (±2%) and 56% (±13%) in the distal small intestine, respectively. Starch digestibility in the stomach and the distal small intestine decreased with increasing level of dietary BG (6% and 0.3% per % dietary BG, $P = 0.006$ and $P = 0.034$, $R^2 = 0.36$ and $R^2 = 0.23$, respectively; Table 4). Apparent protein digestibility in the stomach decreased when BG level increased (3% per % diet BG, $P = 0.017$ and $R^2 = 0.29$).

Physicochemical properties

Dietary BG level affected specific digesta physicochemical properties in all GIT segments except for the proximal small intestine (Table 5). When dietary BG level increased, stomach digesta K (56 Pa × s per % diet BG, $P = 0.003$ and $R^2 = 0.56$), visco45 (2 Pa × s per % diet BG, $P = 0.003$ and $R^2 = 0.38$) and DM content (5 g/kg per % diet BG, $P = 0.0004$ and $R^2 = 0.53$) decreased, whereas n increased (0.02 per % diet BG, $P < 0.0001$ and $R^2 = 0.61$). Digesta WBC increased when dietary BG level increased in both the distal small intestine (0.1 g/g DM per % diet BG, $P = 0.028$ and $R^2 = 0.24$) and distal colon (0.06 g/g DM per % diet BG, $P = 0.024$ and $R^2 = 0.26$). In the proximal colon, visco45 increased when dietary BG level increased (0.1 Pa × s per % diet BG, $P = 0.03$ and $R^2 = 0.24$). Digesta DM content tended to be positively correlated with digesta K in the stomach ($R = 0.42$, $P = 0.07$; Table 6) and small intestine ($R = 0.31$, $P = 0.055$), while significantly positive in the caecum ($R = 0.77$, $P < 0.0001$). In addition, digesta DM content was negatively correlated with digesta n in the stomach ($R = -0.66$, $P = 0.002$), but positively with digesta n in the colon ($R = 0.44$, $P = 0.005$). Digesta K tended to negatively correlate with digesta n in the stomach ($R = -0.42$, $P = 0.07$) and colon ($R = -0.27$, $P = 0.09$), and positively

Table 3 *The effect of dietary β-glucan (BG) level[1] on the mean retention time (min) of digesta solids (TiO_2) and liquids (Cr-EDTA) in the stomach and small intestine of growing pigs estimated using linear regression[2]*

Segment	Variable	Intercept (min)[2]	SE[2]	Slope (min per % diet BG)[2]	SE[2]	P[3]	R^2
Stomach	Solids	126	16.6	−1	2.6	0.796	0.00
	Liquids	39	11.8	6	1.9	0.008	0.35
	Difference	87	7.4	−6	1.2	<0.0001	0.63
Proximal half small intestine[4]	Solids	21	3.8	0	0.6	0.928	0.00
	Liquids	21	4.1	0	0.7	0.989	0.00
	Difference	−0.18	2.1	−0.1	0.3	0.847	0.00
Distal half small intestine[4]	Solids	97	9.8	−2	1.6	0.335	0.05
	Liquids	111	9.9	−2	1.6	0.182	0.10
	Difference	−13	2.8	1	0.5	0.167	0.10
Stomach + small intestine	Solids	250	16.2	−3	2.6	0.255	0.08
	Liquids	177	12.8	3	2.0	0.204	0.09
	Difference[5]	73	8.3	−6	1.3	0.0004	0.53

[1] Dietary BG level ranged from 0% to 10% in five equidistant steps (i.e. 0%, 2.5%, 5%, 7.5% and 10% dietary BG level).
[2] Intercepts and slopes were estimated using linear regression: variable = intercept + slope × BG (% of diet), where the intercept represents estimated value of the dependent variable at 0% BG, and the slope represents the unit of change in the dependent variable per % of BG in the diet. SE = standard error of the estimated intercept and slope.
[3] P-value for H_0: slope = 0.
[4] Division based on total length of small intestine.
[5] Quadratic relation: 99 − 15 × dietary BG level (%) + 0.8 × dietary BG level (%)^2 (P quadratic term = 0.034; R^2 = 0.69; RMSE = 16).

Table 4 *The effect of diet β-glucan (BG) level[1] on the apparent digestibility of starch, and protein (%) in the stomach and small intestine of growing pigs estimated using linear regression[2]*

Segment	Variable	Intercept (%)[2]	SE[2]	Slope (% per % diet BG)[2]	SE[2]	P[3]	R^2
Stomach	Starch	4	12.6	−6	2	0.006	0.36
	Protein	10	6.3	−3	1	0.017	0.29
Proximal half small intestine[4]	Starch	89	5.6	−0.4	0.9	0.638	0.01
	Protein	11	10.9	0.9	2	0.636	0.01
Distal half small intestine[4]	Starch	97	0.7	−0.3	0.1	0.034	0.23
	Protein	58	5.1	−0.5	0.8	0.580	0.02

[1] Dietary BG level ranged from 0% to 10% in five equidistant steps (i.e. 0%, 2.5%, 5%, 7.5% and 10% dietary BG level).
[2] Intercepts and slopes were estimated using linear regression: variable = intercept + slope × BG (% of diet), where the intercept represents the estimated value of the dependent variable at 0% BG, and the slope represents the unit of change in the dependent variable per % of BG in the diet. SE = standard error of the estimated intercept and slope.
[3] P-value for H_0: slope = 0.
[4] Division based on total length of small intestine.

with digesta WBC in the colon (R = 0.29, P = 0.07). Finally, digesta WBC and *n* correlated negatively in the small intestine (R = −0.31, P = 0.09).

Discussion

This study aimed to quantify the relation between diet viscosity, passage kinetics and physicochemical properties of digesta in segments along the GIT. Diet viscosity was induced by the inclusion of isolated oat BG in the diet, ranging from 0% (i.e. BG0) to 10% (i.e. BG10). When mixed with water prior to feeding, the BG0 diet formed an easily pourable suspension from which the solids directly sank to the bottom of the trough if left unstirred, whereas the BG10 diet formed a non-pourable dense dough-like mass. Diet viscosity parameters confirmed that apparent viscosity at 1 and 45/s shear rate (respectively indicated by *K* and visco45) increased when dietary BG level increased.

Although apparent diet viscosity increased when dietary BG level increased, apparent digesta viscosity in the stomach decreased. In addition, liquids remained longer in the stomach when dietary BG level increased (6 min/ % BG in the diet). This together with potentially increasing gastric secretions due to meal viscosity (Rainbird and Low, 1986a; Marciani *et al.*, 2001) resulted in the dilution of stomach digesta in pigs fed diets with increasing BG levels. Based on the high correlation between stomach digesta DM and *K* (this study), and the relation between dynamic viscosity and the volume fraction of particles in suspensions (Konijn *et al.*, 2014) we speculate that the dilution of the stomach digesta explains the decrease in digesta viscosity in pigs fed diets with increasing BG levels. In addition to dilution, depolymerisation of BG in the proximal GIT (Johansen *et al.*, 1993) in high BG diets, and maize starch (Martens, unpublished data) and wheat gluten (George and McCracken, 2002) in low BG diets might have altered their subsequent viscosity-inducing properties. While increasing dietary BG level caused MRT of liquids to increase, the MRT of solids was not affected, in agreement with amongst others Rainbird and Low (1986b). This resulted in a dramatic decrease in the separation of solids and liquids in the stomach when dietary BG level increased.

Table 5 *Linear effect[1] of diet β-glucan (BG) level[2] on digesta viscosity[3] (K, n, visco45), DM content and water-binding capacity (WBC) of the digesta per segment of the gastrointestinal tract in growing pigs*

Variable	Unit	Intercept (unit)[1]	SE[1]	Slope (unit change per % diet BG)[1]	SE[1]	P^4	R^2
Stomach							
K	Pa × s	512	102	−56	16	0.003	0.41
n		0.08	0.03	0.02	0.004	0.000	0.67
visco45	Pa × s	19	4	−2	0.7	0.008	0.35
DM	g/kg	251	7	−5	1	0.000	0.53
WBC	g/g DM	1.1	0.1	−0.01	0.02	0.818	0.00
Proximal small intestine[5]							
K	Pa × s	37	13	−2	2	0.450	0.03
n		0.3	0.08	−0.003	0.01	0.795	0.00
visco45	Pa × s	1.4	0.5	−0.01	0.09	0.902	0.00
DM	g/kg	135	9	−1	2	0.593	0.02
WBC	g/g DM	2.0	0.9	−0.02	0.2	0.893	0.00
Distal small intestine[5]							
K	Pa × s	123	40	−6	6	0.328	0.05
n		0.2	0.02	0.01	0.004	0.127	0.12
visco45	Pa × s	5.2	1.7	−0.2	0.3	0.426	0.04
DM	g/kg	115	8	1	1	0.448	0.03
WBC	g/g DM	1.9	0.3	0.1	0.05	0.028	0.24
Caecum							
K	Pa × s	28	6	0.4	1.0	0.683	0.01
n		0.2	0.03	0.01	0.005	0.061	0.18
visco45	Pa × s	1.0	0.3	0.1	0.04	0.090	0.15
DM	g/kg	119	9	1	1	0.519	0.02
WBC	g/g DM	3.3	0.3	−0.02	0.05	0.723	0.01
Proximal colon[5]							
K	Pa × s	35	5	2	0.9	0.056	0.19
n		0.2	0.03	0.002	0.004	0.668	0.01
visco45	Pa × s	1.8	0.3	0.1	0.05	0.030	0.24
DM	g/kg	193	12	−1	2	0.458	0.03
WBC	g/g DM	2.8	0.3	0.004	0.04	0.933	0.00
Distal colon[5]							
K	Pa × s	34	16	4	3	0.148	0.11
n		0.3	0.06	−0.002	0.01	0.858	0.00
visco45	Pa × s	2.3	1.0	0.3	0.2	0.111	0.14
DM	g/g	252	9	−3	2	0.108	0.14
WBC	g/g DM	2.7	0.1	0.06	0.02	0.024	0.26

[1] Intercepts and slopes were estimated using linear regression: variable = intercept + slope × dietary BG level (% of diet), where the intercept represents estimated value of the dependent variable at 0% BG, and the slope represents the unit of change in the dependent variable per % of BG in the diet. SE = standard error of the estimated intercept and slope. Significant quadratic model (variable = intercept + slope × (dietary BG level × dietary BG level; % of diet) fits were observed for: stomach, $n = 673 - 169 \times$ dietary BG level $+ 11 \times$ dietary BG level^2 (P quadratic term = 0.04; $R^2 = 0.55$; RMSE = 219); stomach, $n = 0.13 - 0.015 \times$ dietary BG level $+ 0.0038 \times$ dietary BG level^2 (P quadratic term = 0.0016; $R^2 = 0.83$; RMSE = 0.045); stomach, visco45 $= 26.1 - 6.89 \times$ dietary BG level $+ 0.47 \times$ dietary BG level^2 (P quadratic term = 0.026; $R^2 = 0.52$; RMSE = 8.66)).

[2] Dietary BG level ranged from 0% to 10% in five equidistant steps (i.e. 0%, 2.5%, 5%, 7.5% and 10% dietary BG level).

[3] Derived from dynamic viscosity by using a power-law function: $= K\dot{\gamma}^{n-1}$, where η = viscosity (Pa × s), $\dot{\gamma}$ = shear rate (/s), n = power law index, K = consistency constant (Pa × s) and visco45 = apparent viscosity at $\dot{\gamma} = 45$/s (Pa × s).

[4] P-value for H_0: slope = 0.

[5] Small intestine and colon were divided in proximal and distal halves based on length.

Apparent digestibility of protein and starch in the stomach decreased when dietary BG level increased. In the case of protein, gastric secretions due to diet viscosity (Marciani *et al.*, 2001) may have increased the contribution of endogenous nitrogen, thereby reducing apparent protein digestibility when dietary BG level increased. In the proximal half of the small intestine no effects of dietary BG level on protein or starch digestibility were observed, while in the distal half of the small intestine, starch, but not protein, digestibility reduced when dietary BG level increased. As the reduction in starch digestibility was not accompanied by increased apparent digesta viscosity or increased protein digestibility, we

Table 6 *Pearson's correlation matrix of the physicochemical properties of digesta[1] in consecutive gastrointestinal tract segments of growing pigs, considering digesta viscosity[2] (K, n), DM content and water-binding capacity (WBC)*

Segment		*K*	*n*	DM	WBC
Stomach	*K*	1			
	n	−0.42†	1		
	DM	0.42†	−0.66***	1	
	WBC	0.23	−0.01	−0.15	1
Small intestine[3]	*K*	1			
	n	−0.23	1		
	DM	0.31†	−0.15	1	
	WBC	0.11	−0.31†	−0.15	1
Caecum	*K*	1			
	n	−0.25	1		
	DM	0.77***	0.01	1	
	WBC	−0.26	−0.04	−0.37	1
Colon[3]	*K*	1			
	n	−0.27†	1		
	DM	0.08	0.44**	1	
	WBC	0.29†	−0.17	−0.22	1

[1] number of observations per variable: 19 in stomach, 20 in caecum (except for WBC:18), 40 in small intestine and colon (except for WBC: 31 and 39 for small intestine and colon).
[2] Derived from dynamic viscosity by using a power-law function: $= K\dot{\gamma}^{n-1}$, where η = viscosity (Pa × s), $\dot{\gamma}$ = shear rate (/s), n = power law index, K = consistency constant (Pa × s).
[3] Combined proximal and distal small intestine or colon segments.
† $P < 0.1$, ** $P < 0.01$, *** $P < 0.001$.

consider it unlikely that this reduction in digestibility can be ascribed to viscosity-inducing properties of BG. Differences in dietary starch source (maize starch *v.* oat starch) and level in the BG0 and BG10 diets might have contributed to the reduction in starch digestibility. Towards the end of the small intestine, most (enzymatic) digestible nutrients are absorbed. This caused concentration of BG contents in digesta to increase, bringing forth increased WBC of digesta in the distal small intestine when dietary BG level increased. The lack of effect of dietary BG level on apparent digesta viscosity in the distal small intestine might be related to the low DM content of digesta in this segment, as described earlier.

Despite BG degradation towards the colon (Johansen *et al.*, 1997; De Vries *et al.*, 2016), concentration of BG in colon digesta likely caused apparent viscosity at 45/s (proximal colon) and WBC (distal colon) of digesta to increase when dietary BG level increased. In addition, other variations in digesta composition in the colon together with the presence and activity of the microbial biomass might have caused variation in observed physicochemical properties of digesta when dietary BG level increased.

In conclusion, the current study showed that when dietary BG level increased, the MRT of liquids, but not that of solids, in the stomach increased. This resulted in a strong reduction in separation of digesta liquids and solids in the stomach, causing dilution of the stomach content. This was illustrated by the decrease in stomach DM content and in turn caused the apparent digesta viscosity to decrease when dietary BG level increased. Effects of dietary BG level on physicochemical properties of digesta in the small intestine were absent and may be related to the low DM content. The water-binding capacity of digesta in the distal small intestine and colon increased with dietary BG level, as did apparent viscosity in the proximal, but not in the distal, colon. These findings likely reflect the concentration of BG in digesta, increasing along the small intestine and decreasing upon their fermentation towards the colon.

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Declaration of interest

The authors declare that there are no conflicts of interest.

Ethics statement

The study was approved by the Dutch Animal Ethics Committee (2014.III.06.056).

Software and data repository resources

None of the data were deposited in an official repository.

Supplementary material

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