

## **Feeding behaviour and pre-prandial status affect post-prandial plasma energy metabolites and insulin kinetics in growing pigs fed diets differing in fibre concentration**

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## **To cite this version:**

Katia Quemeneur, Etienne Labussière, Maud Le Gall, Yannick Lechevestrier, Lucile Montagne. Feeding behaviour and pre-prandial status affect post-prandial plasma energy metabolites and insulin kinetics in growing pigs fed diets differing in fibre concentration. British Journal of Nutrition, 2019, 121 (6), pp.625-636. 10.1017/S0007114518003768 hal-02097211

## **HAL Id: hal-02097211 <https://hal.science/hal-02097211v1>**

Submitted on 11 Apr 2019

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#### **Abstract**

 Variations in feeding behaviour between animals result from individual variations in their metabolism as affected by diet composition*.* The study aimed to link the within-day dynamics of voluntary feed intake and those of blood metabolites and insulin in growing pigs having *ad libitum* access to feed and receiving diets differing in dietary fibre levels and aleurone supplementation*.* Forty pigs (body weight: 35 kg) had access to diets provided ad libitum and 41 differing by fibre content (13 or 18% NDF) and aleurone supplementation (0, 2 or 4  $g/kg$ ). Feeding behaviour was individually recorded during one week. The kinetic of plasma metabolites and insulin was followed during 1 hour after a voluntary test meal*.* Dietary fibre level did not affect daily feed intake but increased meal size and meal duration. Aleurone supplementation (4 g/kg) decreased daily feed intake and number of meals. Dietary fibre level only decreased insulin concentration measured 15 minutes after meal beginning. Aleurone supplementation (4 g/kg) decreased glycaemia during the first hour after the meal and insulinemia 15 minutes after the meal. Free access to feed led to high variability in pre- prandial metabolites and insulin concentrations resulting in different test meal size irrespective of diet composition. Animals were then spread over different profiles combining feeding behaviour and fasted status to explain different profiles of regulation of feed intake*.* Plasma metabolites and insulin kinetics were affected by diet composition but also by animal characteristics. Individual variability should be considered when diet composition is used to modulate feeding behaviour.

Downloaded from https://www.cambridge.org/core. Joby. E Le Gall M. Lechevestrier Montagne L. (2019). Feeding<br>Downloaded from https://www.cambridge.org/core. Jowa State University Library, on 04 Jan 2019 at 16:56:56, subjec behaviour and pre-produced by the pre-produced pre-produced produced plasma energy metabolities and insulin kinetics<br>We haviour and plasma limital produced the program energy metabolites and insulin kinetics and insulin ki

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## **Introduction**

 Dietary fibre (DF) modulates daily voluntary feed intake in association with changes in feeding behaviour: number of meals, meal volume, meal duration and within day spreading of meals <sup>(1)</sup>. In monogastric animals as pigs and humans, these effects may differ according to the origin and composition of DF and body weight (BW) of the subject. As an example, dietary inclusion of sugar beet pulp (Neutral Detergent Fibre (NDF) content =27%) reduced average daily feed intake (ADFI), meal volume and feeding rate whereas inclusion of wheat 63 bran (NDF=23%) did not affect ADFI in pigs of 14 kg BW  $^{(2)}$ . The impact of DF on satiety can be explained either by 1.) dietary energy dilution, 2.) a direct effect due to the increase of digestive content volume with activation of mechanoreceptors, 3.) an indirect effect via metabolic regulation pathways, or 4.) fermentations with a production of short chain fatty 67 acids, as reviewed by Bach Knudsen<sup>(3)</sup> and Li and Patience<sup>(4)</sup>. The variety of animal response to the dietary inclusion of DF suggests that various hormonal, metabolic, physical and microbial pathways are involved in the regulation of feed intake. Testing DF fractions is needed to better distinguish the overall effect of DF on feed intake from the specific and 71 functional properties of some DF fractions  $(3)$ . Wheat aleurone layer, a fraction of wheat bran containing fibres (arabinoxylans and β-glucans) and phenolic compounds, ferulic acids and 73 lignans  $(5)$ , is a suitable candidate as DF-source that can affect glucose and insulin 74 postprandial peaks as demonstrated in horses <sup>(6)</sup>.

 To our knowledge, few studies co-investigated the effect of DF level and the supplementation of a particular fraction of DF on ADFI, feeding behaviour, plasma metabolite and hormone kinetics. Therefore, this current study aimed to link the within-day dynamics of voluntary feed intake, plasma metabolites, and insulin in growing pigs that had *ad libitum* access to feed and received diets differing in DF level and wheat aleurone inclusion. We hypothesized that DF level in the diet and dietary aleurone supplementation modifies feeding behaviour in relation with changes in metabolites and insulin kinetics after a meal, considering that feeding behaviour is closely linked with metabolite and insulin 83 variations  $(7)$ .

 The implication of this study is the modulation of feeding behaviour in pigs. Limiting voluntary feed intake by dietary composition rather than quantitative feed restriction may 86 benefit animal welfare and facilitate increased feed efficiency<sup>(8)</sup>. Due to similitudes in digestion and metabolism between pigs and humans, results obtained in this study also furnished hypotheses regarding human food intake regulation.

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## **Methods**

 The experiment was performed at the INRA experimental facilities in Saint-Gilles (France) (agreement number: C35-275-32) in compliance with the French directive on animal experimentation and care (2013-118) after evaluation by a competent ethical committee in animal experimentation under the responsibility of the French ministry of research (authorization number 2016072907418869).

## **Animals, housing and experimental design**

96 The experiment was conducted with forty castrated males ((Pietrain  $\times$  (Large White  $\times$ 97 Landrace)) with an average initial BW of  $25.6 \pm 3.0$  kg (70 days of age). To avoid pain and perturbations during time-series blood sampling, a catheter was inserted in the external jugular vein through a collateral vein according to a protocol previously described by 100 Melchior et al.  $^{(9)}$  under general anaesthesia (ketamine and isoflurane). After the surgery, pigs had two weeks of recovery and adaptation to experimental diets and to individual housing. 102 Then, pigs were weighed and individually housed in a metabolic cage ( $60 \times 120$  cm) with 103 metal floor placed in an enclosure  $(1.7 \text{ m}^3)$  and equipped with a weighing scale in order to continuously record feed consumption during seven days. The study was conducted during thirteen batches of three or four littermates each. For each batch, the three or four littermates with a similar BW were selected and successively housed during one week in the enclosure as only one was available. The temperature in the enclosure was maintained constant at 24°C and a 12h lighting time span (0730 to 1930 hours) was used. Each pig had free access to water and one of the six experimental diets. During all the experiment, animals were carefully observed to detect potential injures of welfare and disease.

**Experimental diets**

 Two concentrations of DF (low fibre: LF (NDF=10%) and high fibre: HF (NDF=15%)) and three levels of aleurone supplementation (GrainWise Wheat Aleurone; Horizon Milling; Minneapolis, Minnesota, United States of America; 0 g/kg: A0, 2 g/kg: A2 and 4 g/kg: A4) were tested in six experimental diets (table 1). The HF diet contained a mixture composed of 50% of wheat bran, 33% of soya hulls and 17% of sugar beet pulp. This mixture of three DF- rich feedstuffs having different physicochemical properties permitted to study an overall 118 effect of DF level rather than the effect of DF from a specific source  $(3)$ . Experimental diets were balanced on the ratio of digestible lysine to net energy (NE). Energy content was lower in the HF diets due to the introduction of DF (-6% of NE per kg of dry matter (DM) for HF 121 diet  $(10)$ .

 Pigs received 500 g of a commercial growing feed (NDF=14%) on the first day after the surgery, and then 1000 g per day during four days with a transition from the commercial diet they fed before surgery to one of the six experimental diets (80%/20%, 60%/40%, 40%/60%, 20%/80%). One level of DF with its three levels of aleurone supplementation was tested within each batch. Pigs had free access to experimental diets between 0900 and 1630 and between 1700 and 0600 that permitted mimicking an *ad libitum* feed intake at the scale of the day. Each day, feed allowance was determined to be greater than voluntary daily feed intake. To avoid feed spillage, feed was provided twice a day at 0845 and at 1645, before trough emptying. The daily feed allowance was weighed and a sample of offered feed was cumulated each day of measurements for each pig for immediate DM measurement. For each experimental diet, samples were pooled over the whole experiment for chemical analyses. Feed refusals and spillages were collected at the end of each week of measurements and were oven-dried to determine the refused DM.

## **Feeding behaviour recording**

 After one day of adaptation in the enclosure, feeding and drinking behaviour were analysed during the 6 following days. For feed intake calculations, a day of measurement began at 0900 and finished at 0600. For water intake calculations, a day of measurement began at 0900 and finished at 0800 to take into account water meals when the feed trough was locked. The feed trough and the water container were on a weighing scale for recording feeding and drinking behaviour. The water container was filled each morning with tap water. The weight of the feed trough and the water pit was recorded every 10 seconds. A consumption of feed was defined as a negative variation of the weight of the feed trough. The feed intake size was calculated as the difference between the stabilized weight of the trough before and after the variation. The feed intake duration was defined as the duration between the beginning and the end of the weight variation. In order to compare our results with other studies, successive feed bouts were grouped into the same meal using a meal criterion defined 148 as the maximum length between two feed bouts owing to the same meal  $(11)$ . Feed bouts separated by intervals shorter than the meal criterion were considered to be part of the same meal and were clustered accordingly. The size of a meal was the sum of the size of the feed bouts and the duration of the meal was the duration between the beginning of the first feed bout and the end of the last feed bout of the meal. In our study, the meal criterion was 153 estimated using the log curves technique  $(12)$  and was established at four minutes. The DM feed intake per meal was calculated as the feed intake per meal adjusted for the percentage of

 DM of the feed measured weekly for each pig. Meals with a size below 10 g were not kept for statistical analysis but spread over other meals of the day. The ADFI, expressed in g of DM per day, was calculated for each pig as the average of dried feed intake from the 6 days considered in the analysis. From the generated database, daily number of meals, average feed intake per meal (g of DM), average duration per meal (min), daily feed intake (g of DM per day) and total ingestion duration per day (min) were calculated as indicators of feeding behaviour. Daily total water intake was calculated as the difference of the water container weight during 23-h periods.

## **Blood collection**

 On day 7, blood was sampled to analyse metabolites and insulin plasmatic concentrations. The catheter was externalized outside of the enclosure and permitted to collect blood samples without disturbing the animal. The first meal of day 7 was considered as a test meal. Blood (10 mL) was sampled at 0830 and 0845 (referred as pre-prandial), at the beginning of the meal and 15, 30, 45, 60 minutes after the beginning of the meal. Blood samples (10 mL per sample; 5 mL collected on EDTA and 5 mL collected on heparin) were stored on ice before centrifugation during 10 min at 3000 g (4°C). Plasma was separated into aliquots and stored at -20°C until metabolites and hormone concentration analyses. For each blood sampling, the haematocrit (H) was measured and a basal haematocrit (BH) was calculated as the mean of pre-prandial haematocrits of this pig. Plasma metabolite and insulin concentrations were adjusted as follows to take into account possible dilution because of water intake and saline solution perfusion to flush the catheter line between successive samplings:

$$
Adjusted\ concentration = Real\ concentration \times \frac{(100 - BH)}{(100 - H)}
$$

### **Chemical analyses**

 The experimental diets were analyzed for DM, ash, gross energy, nitrogen, ether extract, crude fibre, different fibre fractions (NDF, ADF, ADL) and starch according to standard 179 procedures <sup>(13)</sup>. Commercial kits were used to determine plasma concentrations of glucose (Glucose RTU; bioMérieux, Craponne, France), lactate (Lactate PAP; bioMérieux, Craponne, France), free fatty acids (NEFA-HR(2); Wako Chemicals GmbH, Neuss, Germany), urea (Urea UV 250; bioMérieux, Craponne, France), α-amino nitrogen (Protéines-kit; bioMérieux, Craponne, France) and triglycerides (Triglycérides Enzymatique PAP 150; bioMérieux, Craponne, France). These parameters were measured with a Konelab 20i device (Thermo

 Fisher Scientific, Courtaboeuf, France) according to manufacturers' recommendations. Plasma concentrations of insulin were measured using an RIA kit (INSULIN-CT; CisBio Bioassays, Codolet, France). Intra-assay CV was less than 5%.

**Data analyses**

 The NE concentration of the diets was calculated with the equation NE=0.703×DE+1.58×EE+0.47×ST-0.97×CP-0.98×CF with DE for Digestible Energy, EE for Ether Extract, ST for Starch, CP for Crude Protein and CF for Crude Fibre<sup>(10)</sup> 

 Based on feeding behavior, between four to eight animals per treatment are necessary to achieve the statistical power of 90% with an alpha level at 5% to see a difference of 100 g on ADFI and a difference of 2 meals per day.

 Pigs were individually housed in an enclosure. A batch was constituted by 3 or 4 littermates that were successively measured during one week each. One level of DF and three levels of aleurone supplementation were tested during one batch and the other level of DF (with its three levels of aleurone supplementation) was tested during the following batch. For the last replicate, 4 littermates were used, fed with LF-A0, LF-A2, LF-A4 and HF-A0 to adjust number of pigs per treatment.

 The analysis thereafter was conducted using linear mixed model with the MIXED procedure of SAS (SAS Inst. Inc., Cary, NC) and the assessment of significance of the factors tested in each model was based on "Type 3 tests of fixed effects" as experimental design is not strictly balanced. For variables considered as repeated effect, the REPEATED statement 205 was used in the procedure. An unstructured covariance matrix (type  $=$  UN) was used for these models, because it was the covariance structure that displayed the lowest AIC and BIC in comparison with other covariance structure that were tested (compound symmetry, Toeplitz or autoregressive). Data were tested for normality according to Shapiro-Wilk's test of residual.

 Variables describing feeding behaviour (ADFI, NE intake, number of meals, meal size, meal duration and average interval between two meals) were analysed in a linear mixed model with levels of DF, levels of aleurone and their interaction considered as main factors, batch as a random factor and day of the week as a repeated effect with the pig as the experimental unit.

 Water intake per day was analysed in a linear mixed model with levels of DF, levels of aleurone and their interaction considered as main factors, feed intake level and number of

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217 meals per day as covariates, batch as a random factor and day of the week as a repeated effect 218 with the pig as the experimental unit.

219 Only data from pigs (n=26) that were fed two voluntary meals between 0900 and 1700 on 220 the day of blood kinetic were considered in the statistical analysis of plasma metabolites and 221 insulin concentrations.

 Pre-prandial plasmatic concentration of metabolites (glucose, lactate, free fatty acids, 223 triglycerides, urea and  $\alpha$ -amino nitrogen) and insulin were analysed in a linear mixed model with levels of DF, levels of aleurone and their interaction considered as main factors, the interval since the last meal and the size of this last meal as covariates, batch as a random factor and time as a repeated effect with the pig as the experimental unit.

 Plasma metabolites and hormone concentrations were analysed in a linear mixed model with levels of DF, levels of aleurone and their interaction considered as main factors, the size 229 of this test meal (expressed as  $g/kg$  BW $^{0.60}$ ) and pre-prandial concentration of analysed metabolites as covariates, batch as a random factor and time as a repeated effect with the pig as the experimental unit. When the effect of interaction between time and DF level or aleurone supplementation were significant, post hoc tests were performed through Tukey's pairwise comparison of the means for each time. LS-means were calculated to obtain adjusted means from the statistical model. When data are unbalanced, LS-means give better mean estimates than simple means (LSMEANS statement in SAS).

236 Data were further analysed by multiple factorial analysis and hierarchical classification 237 on principal components to discriminate clusters of pigs using of the R statistical package 238 "FactoMineR"  $(14)$ . As blood metabolites and insulin concentrations are affected by feeding 239 behaviour  $(7; 15)$ , size of the test meal and pre-prandial metabolites and insulin concentrations, 240 pigs were discriminated on these different factors of variation to analyse their effects on 241 plasma metabolites and insulin kinetics. Three classes of variables were included in the 242 analysis: pre-meal plasma concentrations of metabolites (glucose, lactate, free fatty acids,  $\alpha$ -243 amino nitrogen, urea and triglycerides) and insulin; variables characterizing feeding behaviour 244 (number of meals, average meal size (g/kg  $BW^{0.60}$ ), average duration of meal (minutes), total 245 duration of feed intake per day (minutes); and ADFI ( $g/kg BW^{0.60}$ )) and the size of the test 246 meal (g/kg BW $^{0.60}$ ). After cluster identification, data were further tested by linear mixed 247 model as previously described replacing the DF, aleurone supplementation effects and their 248 interaction by a cluster effect.

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 Data for pre-meal insulin concentration and concentrations of glucose, insulin, urea, free fatty acids and triglycerides during the hour after the test meal were log-transformed before statistical analyses.

 Differences between treatments were considered significant for *P*<0.05 whereas 0.05<*P*<0.10 was discussed as a trend. Data are shown as least-squares means in tables and means in graphics with the residual square deviation (RSD) as an indication of the variability.

#### **Results**

 Two pigs fed the LF-A0 and HF-A4 diets exhibited fever associated with a low ADFI on the week of measurements. They were excluded from the experiment and subjected to antibiotic treatments (150 mg Amoxicillin per 10 kg for BW). Consequently, 38 pigs were considered in the final analysis. Only the data from 26 pigs that were fed two voluntary meals between 0900 and 1700 on the day of blood kinetic were considered in the statistical analysis of plasma metabolites and insulin concentrations.

## *Influence of diets on feeding behaviour.*

 There was no interaction between DF level and aleurone supplementation on any variables characterizing feed intake and feeding behaviour. Pigs had less (*P*<0.01) but larger (+19%, *P*<0.01) meals with high level of DF, without effect on ADFI and NE intake (table 2). Whereas average meal duration (+10%, *P*<0.01) and interval between two meals increased (+14%, *P*<0.01) with DF level, the total daily feed intake duration was similar. The decrease 268 in ADFI (-20%, when compared with other diets; *P*<0.01) for aleurone supplementing diet (4 g/kg) was associated with a decreased number of meals per day (*P*<0.01). Pigs spent less time per day to eat and interval between two meals was extended (*P*<0.01) with diets supplemented with 4 g/kg of aleurone. Neither DF level nor aleurone supplementation modified total water intake, considering feed intake and number of meals as covariates.

*Influence of diets on plasmatic metabolites and insulin concentrations.*

 There was no interaction between DF level and aleurone supplementation on pre-prandial plasmatic concentration of metabolites and insulin. High level of DF decreased pre-prandial insulin concentration (*P*=0.01) and tended to decrease pre-prandial glucose concentration (*P*=0.06) when compared with the diets with low level of DF (table 3). The pre-prandial insulin concentration was the greatest with aleurone supplemented diet at 2 g/kg compared to 279 others aleurone supplementations  $(P<0.01)$ . The pre-prandial α-amino-nitrogen concentration was lower with aleurone supplemented diet at 4 g/kg (*P*=0.04). Pre-prandial lactate, urea, free fatty acids and triglycerides concentrations were not affected by the dietary factors. An

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 increase of the interval between the test-meal and the last meal decreased pre-prandial concentration of insulin (*P*<0.01) and increased pre-prandial free fatty acids concentration (*P*=0.05) whereas an increase of the size of the last meal increased pre-prandial concentration of insulin (*P*<0.01) and decreased pre-prandial free fatty acids concentration (*P*=0.04).

 The size of the voluntary test meal was greater with high level of DF (368 vs 242 g of 287 DM,  $P=0.04$ ) and longer (19.4 min. vs 13.8 min., P=0.02). It was not modified with aleurone 288 supplementation (data not shown). Except for urea concentration (P=0.18), concentrations of all metabolites and insulin significantly changed during the first hour after the test meal (*P*<0.01, figure 1). During the first hour, there was no interaction between DF level and aleurone supplementation for α-amino-nitrogen, urea, free fatty acids and insulin concentrations and only a tendency for glucose and lactate concentrations (*P*=0.08). Moreover, triglycerides concentration was lower for HF-A4 diet than for any other diets (*P*=0.02; figure 2). Dietary fibre level did not affect any kinetics of metabolites and insulin throughout the first postprandial hour whereas aleurone supplementation decreased glycemia (*P*<0.01; figure 1(b)). Insulin concentration at 15 minutes after the meal was lower for pigs 297 fed high level of DF ( $P=0.03$ ) and was lower for pigs fed aleurone supplemented diet ( $4 \frac{g}{kg}$ ) 298 than pigs fed diet without aleurone supplementation  $(P=0.04)$ .

## *Characterization of clusters.*

 Two principal components accounting for 49% of total variance among pigs were retained from the multiple factorial analyses with 30% for the first component and 19% for the second component. Contributions of each variable to these two major components are presented in table 4. Based on the multiple factorial analyses, the hierarchical classification discriminated pigs according to four clusters. Dietary treatment only partially agreed with cluster classification (table 5). Clusters 1 and 2 grouped the lightest pigs (34.9 and 37.5 kg, respectively) having low ADFI (1209 and 1174 g/d, respectively) and few number of meals per day. Clusters 3 and 4 grouped the heaviest pigs (44.9 and 43.0 kg, respectively) having high ADFI (1580 and 1838 g/d, respectively) and a large number of meals per day. Additionally, pigs grouped in cluster 4 ate a more important voluntary test meal than those grouped in other clusters (*P*<0.01). Pre-prandial plasma concentration of free fatty acids was greater for pigs in clusters 1 and 3 than for pigs in clusters 2 and 4 (*P*<0.01). Pre-prandial α- amino-nitrogen concentration varied from 516 mg/L for pigs from cluster 1 to 762 mg/L for pigs from cluster 4 (*P*<0.01). Mean urea concentration varied from 112 mg/L for cluster 2 to 195 mg/L for cluster 1 (*P*<0.01).

 During the first hour after the meal, glucose, lactate, triglycerides and insulin kinetics did 316 not differ between clusters whereas free fatty acids,  $\alpha$ -amino nitrogen and urea concentrations were affected (figure 3). Free fatty acids concentration was greater for pigs grouped in clusters 1 and 3 than for pigs grouped in clusters 2 and 4 (*P*<0.01; figure 3(d)). Concentration of α-amino nitrogen increased between pigs in cluster 1 and pigs in cluster 4 (*P*<0.01; figure 3(e)). Urea concentration was higher for pigs grouped in clusters 1 and 4 than for pigs 321 grouped in clusters 2 and 3  $(P<0.01$ ; figure 3(f)).

## 322 **Discussion**

 Dietary fibre level or aleurone supplementation modified feeding behaviour and blood and insulin kinetics in pigs having free access to feed during 20.5 hours per day. No interaction between DF level and aleurone supplementation was found. Dietary fibre level did not affect 326 ADFI but increased meal size  $(+ 28 \text{ g})$  and meal duration  $(+ 1 \text{ min})$  while reducing the number of meals per day (-1 meal). Aleurone supplementation (4 g/kg) decreased ADFI (- 314 g) and the daily number of meals (-1.5 meals per day). These results suggest differences in the importance of each regulation pathways (digestive, metabolic, hormonal and microbial regulations) of voluntary feed intake between the two dietary strategies that were tested to affect feeding behaviour.

 In pigs fed diets enriched in DF diluting energy concentration (-25% of digestible energy), regulations of voluntary feed intake often lead to increased ADFI (+850 g of DM) to satisfy 334 energy requirements (16). In our study, DF enrichment, diluting the NE concentration by only 6% when compared with the control diet, did not reduce ADFI. Similarly, a NE dilution of 336 5% did not modify feed intake in growing pigs between 35 and 50 kg of BW  $^{(17)}$ . Nevertheless, HF diet modified feeding behaviour, with pigs eating fewer meals per day of greater size than pigs fed the LF diet. The reduction of meal frequency with HF diet was in accordance with previous studies showing that introduction of DF can increase satiety and 340 delay the initiation of the next meal  $(18)$ . This delay could be due to the production of short 341 chain fatty acids by microbial bacteria, using DF as substrates for fermentation <sup>(19)</sup>. Meal size is partly regulated by activation of mechanoreceptors and the distension of the stomach 343 leading to an early volumetric satiety  $(20)$ . With the HF diet and its bulking properties, meals were expected to end sooner, resulting in smaller meal size due to an earlier stimulation of mechanoreceptors after meal onset. In our study, greater meals suggest that this regulation pathway was not enhanced with HF diet compared with LF diet and a possible adaptation of 347 stomach to counteract the physical volumetric effect of DF $^{(21)}$ . Physical effects of DF on meal

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 size depend on the introduction rate and nature of fibrous sources, on the BW of the pig, and 349 on the duration of the adaptation period to the DF-rich diet  $(2, 22)$ . In the present study, a mixture of three DF sources (wheat bran, sugar beet pulp and soya bean hulls) with different physical properties was used to test an overall DF effect rather than the consequences of a 352 specific property  $^{(22)}$ . In addition, the BW of pigs (37 kg) and the adaptation period (2 weeks) were probably sufficient to satisfactorily adapt the digestive tract of the pigs with an increase of the empty stomach weight (276 g vs 293 g for LF and HF diets respectively, *P*<0.01, data not shown). Moreover, meal size and duration are also regulated by metabolite concentrations 356 as suggested by the glucostatic theory of feed intake regulation  $(23)$ . In our study, this metabolic regulation could be more important than bulking effect of high DF level. With DF 358 level, longer  $(+ 1 \text{ min})$  and greater  $(+28 \text{ g})$  meals may be explained by a longer duration to reach glucose homeostasis. At the end of the meal (13.8 min vs 19.4 min for pigs fed LF and HF diets respectively), although glycaemia did not significantly differ between HF and LF diets (1112 and 1050 mg/L for pigs fed LF and HF diet respectively, as predicted from the 362 kinetics of plasma metabolites, *P*=0.28), insulinemia was lower for HF diet than LF diet (15.2) mUI/L and 8.2 mUI/L, for pigs fed LF and HF diet respectively, *P*=0.05). In the present study, the three fibre sources used in the HF diets are known to delay gastric emptying and to 365 reduce digestibility of starch sources  $(24)$ . Increased duration of meals may thus permit to pigs to reach glucose homeostasis. The delayed end of the meal may be due to the lower concentration of insulin with DF level, which underlines the importance of some hormones in regulation of feed intake.

 The decrease in NE intake with aleurone supplementation (4 g/kg) suggested that regulations of ADFI did not result in a constant intake of NE in all cases. The decreased ADFI was explained by a decreased meal number without increase of meal size. This result suggests 372 an extension of satiety which could be partially explained by microbial activity  $(25)$ . In our study, postprandial free fatty acids concentration tended to be lower with aleurone supplementation during the first 45 min after the meal. Short chain fatty acids decrease free 375 fatty acid concentrations with a possible inhibition of hormone-sensitive lipase  $(26)$ . As 376 suggested in previous studies in pigs  $(27)$  and rats  $(28)$ , wheat aleurone-rich flour increased short chain fatty acids production in the caecum and colon as the consequence of arabinoxylan fermentation. Short chain fatty acids can be used as energy substrate (up to 14% of pig 379 maintenance requirements  $(29)$  and they can modify long term energy homeostasis  $(30)$ . Short chain fatty acids stimulate satiety hormones like GLP-1 or PYY, thus inhibiting the initiation

(6), 625-636. , DOI : 10.1017/S0007114518003768

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381 of a next meal  $(31, 32)$ . Satiety can also be linked to a period of elimination of metabolic waste 382 resulting from hepatic oxidation and nitrogen metabolism<sup>(33)</sup>. Regulation of metabolic waste elimination occurs probably more than one hour after the meal. Because urea concentration did not differ between treatments, the present results did not support this hypothesis. The increase of the interval between meals also observed with high DF level might partially result from similar mechanisms due to the presence of aleurone in DF-rich diets that contain wheat and wheat bran.

 The different pathways permitting the regulation of feed intake (digestive, hormonal, metabolic or microbial) coexist but their relative importance at a specific time might depends on diet composition (DF, aleurone) and animal characteristics. In our trial, as pigs had free access to feed during 22.5 hours of the day, an important variability in feeding behaviour between pigs was observed. The daily number of meals ranged from 2 to 31 and the meal size ranged from 69 g to 379 g DM ingested per meal. In most of the experiments studying metabolite or hormone kinetics, animals were fasted during at least 12 hours before receiving 395 a test-meal of a fixed amount  $(34)$  whereas in commercial farms, pigs do not have similar ADFI or feeding behaviour. Consequently, it is needed to let pigs eat with constraints as limited as possible to assess the importance of each regulation mechanism behind this variability to optimize nutritional solution. On the day of blood kinetics measurements, the interval between the meal preceding the test meal and the test meal varied from 115 to 911 minutes. The size of this last meal varied from 21 to 385 g of DM. Pigs did not have the same metabolic status at the beginning of the kinetic measurements. Pre-prandial glycaemia ranged from 689 to 1201 mg/L and pre-prandial free fatty acids concentration ranged from 45 to 485 µmol/L. Moreover, as the test meal was a voluntary meal, its size was extremely variable between animals, ranging from 98 to 710 g of DM. This variability of feeding behaviour as well as pre-prandial concentrations of metabolites and insulin induced different responses after the voluntary test meal. Apart from a direct analysis of variance according to the experimental design, a discriminant analysis leading to clustering of animals was attempted to aggregate animals in groups with similar pre-prandial metabolic status. Metabolic responses of pigs grouped in cluster 3 exhibited a large increase of glycaemia and insulinemia after the ingestion of the meal test and fitted to metabolic responses of control groups in other studies  $(7; 35)$ . These animals had almost 9 hours of fasting before the beginning of the kinetic measurements and they were fed the LF diet without aleurone supplementation, leading to usual basal conditions before feeding. Cluster 2 grouped pigs that were fed the HF diet or

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 aleurone supplementing diets. The low level of free fatty acids during the first hour after the meal might be explained with the low pre-prandial concentration of free fatty acid and with the production of short chain fatty acids which are known to decrease free fatty acids 417 plasmatic concentrations  $(26)$ . This underlines the importance of microbial activity in changes of feeding behaviour due to DF level. An increase of meal frequency (cluster 4) induced changes of regulation pathways of feed intake. In this cluster, pigs fed different experimental diets suggesting that animal characteristics could be more important than diet composition in some post-prandial responses. This result is in accordance with another study which showed 422 an important variability of feeding behaviour in the same group  $(36)$ . Despite a low level of plasma free fatty acids, these pigs had a heavier test meal than pigs of the other clusters, which might be due to the heavy BW of animal suggesting a larger stomach and ingestion 425 capacity. The large meal size was associated with a high concentration of  $\alpha$ -amino nitrogen whereas glucose and insulin responses were less modified. Although not significant, our results are in accordance with others studies that exhibited less daily fluctuations of glucose 428 and insulin with increased meal frequency  $(7, 37)$ . Other studies reported that kinetics on 429 glucose did not only depend on diet composition but also of feeding behaviour  $(38)$ . We supposed that frequent meals induced a continuous supply of glucose and other nutrients without important fluctuations of their plasmatic concentration. Glucose metabolism may not be the first regulation pathway which modulates feed intake in these pigs. Finally, whereas 433 others clusters showed a large test meal size  $(> 220 \text{ g})$  compared with average meal size over the measurement period (< 200 g), pigs grouped in cluster 1, fed predominantly LF diet, showed a test meal more representative of the averaged meal size over other days. As pigs belonging to this cluster were light (34.9 kg), their ingestion capacity may be limited. Due to 437 the small meal size, pigs presented a low  $\alpha$ -amino-nitrogen concentration associated with high urea concentrations in pre-prandial situation and one hour after the meal. These results suggest that pigs mobilized protein storages to meet energy requirements.

 To conclude, there was no interaction between DF level and aleurone supplementation on feeding behaviour in growing pigs. Dietary fibre level in the diet increased meal size and decreased daily meal number without affecting ADFI whereas aleurone supplementation decreased ADFI with a reduction of the meal number per day. The dietary supplementation with wheat aleurone modulated feed intake with effect of satiety regulation pathways, when introduced at 4 g/kg in the diet. Moreover, this trial permitted to show that the variability of feeding behaviour and metabolic responses when pigs have *ad libitum* access to feed might be

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 due to different regulation pathways with different degrees of importance depending on diet composition and animal characteristics. Inter-individual variability should be considered when diet composition is used to modulate feeding behaviour.

## **Acknowledgments**

 The authors thank G. Guillemois and J.F. Rouaud for diets manufacturing, S. Dubois, A. Chauvin, J. Georges, F. Le Gouevec, M.H. Lohat and V. Piedvache for animal care and R. Comte, Y. Jaguelin, A. Marchais, C. Perrier and G. Robin for laboratory analyses. The authors thank R. Resmond for his help when writing the statistical section.

## **Financial support**

 This work was financially supported by Provimi France - Cargill (Crevin, France) with the number of contract: 2016/0019 (Cifre scheme; Cifre = Conventions Industrielles de Formation par la Recherche – industrial research training agreements for PhD students). Provimi France also provided support in the form of salaries for some authors (M. L. G., K. Q., and Y. L.).

## **Conflict of interest**

 E. L. and L. M. had no conflict of interest. M. L. G., Y. L. are permanent salaries and K.Q. contractual salaries (3 years) from Provimi France that is a part of the Cargill Group. The wheat aleurone tested in the study is commercialized by Horizon Mills that is also a part of the Cargill group (Minneapolis, Minnesota, United States). M. L. G., Y. L. participated to the funding of this work, to the discussion of the results and to the reviewing of the manuscript but did not have any additional role in the study design, data collection and analysis, and decision to publish, or preparation of the manuscript.

### **Authorship**

 K. Q., E. L., L. M. designed the study. K. Q., with direction from E. L. and L. M., was responsible for data collection and statistical analysis. E. L. assisted with the study execution. E. L. and L. M. reviewed the manuscript and M. L. G. and Y. L. participated to the reviewing of the manuscript. All authors read and approved the final manuscript. L. M. is the corresponding author.

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ridge.org/core/terms: https://doi.org/10.1017/3000/114518003/68 Presentration. British Journal of Nutrition, 121<br>In growing pigs fed diets differing in fibre concentration. British Journal of Nutrition, 121 (6), 625-636. , DOI : 10.1017/S0007114518003768

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Ingredients (g/kg of DM)

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## 563 **Table 1**. Ingredients and chemical composition of the experimental diets

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A0, no aleurone; A2, supplementation of 2 g/kg of aleurone; A4, supplementation of 4 g/kg of 565 aleurone; DM, dry matter

566 † GrainWise Wheat Aleurone, Horizon Mills, Cargill, Minneapolis, Minnesota, United States

567 with 19.3 MJ gross energy/kg DM, 18.5% DM of crude protein, 11.1% DM of crude fibre and

- 568 52.6% DM of neural detergent fibre.
- 569 ‡ The premix supplied (per kg diet) for LF diet: -lysine HCL, 3 g; L-threonine, 1 g, L-570 tryptophan, 0.1 g; DL-methionine, 0.4 g; salt, 4.5 g; calcium carbonate, 5.9 g; dicalcium
- 
- 571 phosphate, 10.1 g; vitamin A, 5000 UI; vitamin D3, 1000 UI; vitamin E, 20 mg; vitamin B1, 2

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572 mg; vitamin B2, 4 mg; pantothenic acid, 2000 mg; vitamin B6, 1 mg; vitamin B12, 0.022 mg;

- 573 niacinamide, 15 mg; vitamin K3, 2 mg; folic acid, 1 mg; biotine, 0.2 mg; choline chloride, 50
- 574 mg; Mg, 0.1 g; Ca, 1.33 g; Fe, 80 g; Cu, 10 mg; Zn, 100 mg; Mn, 40 mg; I, 0.2 mg; Se, 0.15
- 575 mg and for HF diet and L-lysine HCL, 2.8 g; L-threonine, 0.9 g, L-tryptophan, 0.1 g; DL-
- 576 methionine, 0.4 g; salt, 4.5 g; calcium carbonate, 4.7 g; dicalcium phosphate, 9.9 g; vitamin
- 577 A, 5000 UI; vitamin D3, 1000 UI; vitamin E, 20 mg; vitamin B1, 2 mg; vitamin B2, 4 mg;
- 578 pantothenic acid, 2000 mg; vitamin B6, 1 mg; vitamin B12, 0.022 mg; niacinamide, 15 mg;
- 579 vitamin K3, 2 mg; folic acid, 1 mg; biotine, 0.2 mg; choline chloride, 50 mg; Mg, 0.1 g; Ca,
- 580 1.33 g; Fe, 80 g; Cu, 10 mg; Zn, 100 mg; Mn, 40 mg; I, 0.2 mg; Se, 0.15 mg.
- 581 § The net energy (NE) was calculated with the equation NE=0.703×DE+1.58×CF+0.47×ST-
- 582 0.97×CP-0.98×CF<sup>(9)</sup> with DE for Digestible Energy, EE for Ether Extract, ST for Starch, CP
- 583 for Crude Protein and CF for Crude Fibre<sup>(9)</sup>

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584 **Table 2**. Effect of dietary fibre and aleurone supplementation on feeding and drinking



585 behaviour in growing pigs

586 A0, no aleurone; A2, supplementation of 2 g/kg of aleurone; A4, supplementation of 4 g/kg of 587 aleurone; DM, dry matter; HF, high fibre; LF, low fibre; NE, net energy.

588 The experiment was conducted with 5 growing pigs fed LF-A0, 7 growing pigs fed LF-A2, 6 589 growing pigs fed LF-A4, 8 growing pigs fed HF-A0, 7 growing pigs fed HF-A2 and 5 growing pigs fed HF-A4. <sup>590</sup>

591 a,b Mean values within a column with unlike superscript letters were significantly different 592 (P<0.05).

 † Analysis of variance performed using Proc Mixed (SAS) including effects of dietary fibre (F), aleurone (A), interaction between dietary fibre and aleurone (non-significant) and day (non-significant). Data are presented in table as least squares means (*lsmeans* statement in 596 SAS).

597 ‡ RSD= residual standard deviation.

598 § Logarithmic transformation was previously performed to validate normality test according 599 to Shapiro-Wilk's test of residual. Values are presented in table as means of the estimated

600 data from MIXED model after exponential transformation of the predicted values. Residual

601 standard deviation of these variables is calculated as the standard error of the difference 602 between experimental data and estimated data.

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603 **Table 3**. Effect of dietary fibre and aleurone supplementation on pre-prandial concentrations 604 of plasma metabolites and insulin in growing pigs

		Fibre	Aleurone			P <sub>†</sub>				
	LF	<b>HF</b>	A <sub>0</sub>	A2	A4					
Number of pigs	14	12	9	9	8	<b>RSD¶</b>	$\mathbf{F}$	$\mathbf{A}$	$\mathbf I$	LMS
Insulin (mUI/L) $\S$	5.8	3.1	$3.7^{a}$	$6.7^{b}$	3.0 <sup>a</sup>	2.1	0.01	< 0.01	< 0.01	< 0.01
Glucose $(mg/L)$	1183	1102		1152 1156 1118		88	0.06	0.70	0.08	0.25
Lactate $(\mu mol/L)$	930	882	905	894	919	162	0.50	0.95	0.22	0.46
Free fatty acid (mol/L)	185	143	134	179	179	98	0.34	0.59	0.05	0.04
Triglycerides (mg/L)	257	285	288	286	238	70	0.37	0.35	0.75	0.47
$\alpha$ -amino nitrogen										
(mg/L)	645	671		$697^{\degree}$ 701 <sup>a</sup> 576 <sup>b</sup>		95	0.54	0.04	0.90	0.53
Urea $(mg/L)$	185	161	164	155	199	40	0.20	0.13	0.17	0.32

 $A0$ , no aleurone; A2, supplementation of 2 g/kg of aleurone; A4, supplementation of 4 g/kg of 606 aleurone; DM, dry matter; HF, high fibre; LF, low fibre

 $F_{607}$  The experiment was conducted with 5 growing pigs fed LF-A0, 4 growing pigs fed LF-A2, 5 growing pigs fed LF-A4, 4 growing pigs fed HF-A0, 5 growing pigs fed HF-A2 and 3 <sup>608</sup> growing pigs fed HF-A4. <sup>609</sup>

610 a,b Mean values within a column with unlike superscript letters were significantly different 611 (P<0.05).

 † Analysis of variance performed using Proc Mixed (SAS) including effects of dietary fiber (F), aleurone (A), interaction between dietary fiber and aleurone (non significant), interval since the last meal (I) and the size of the last meal (LMS). Data are presented in table as least squares means (*lsmeans* statement in SAS).

616 ‡ RSD= residual standard deviation.

617 § Logarithmic transformation was previously performed to validate normality test according

618 to Shapiro-Wilk's test of residual. Values are presented in table as means of the estimated

619 data from MIXED model after exponential transformation. Residual standard deviation of

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- 620 these variables is calculated as the standard error of the difference between experimental data
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622 Table 4. Contributions<sup>1</sup> of each variable to components 1 and 2 in the Multiple Factorial 623 Analysis performed on pre-prandial plasmatic metabolite and insulin concentrations and 624 feeding behaviour in growing pigs

	Component 1	Component 2
Voluntary meal size	36.3	11.9
Pre-prandial plasmatic concentration		
$\alpha$ -amino-nitrogen	20.2	0.0
Triglycerides	5.9	11.8
Glucose	5.7	4.7
Free fatty acids	1.9	21.3
Lactate	1.1	21.1
Urea	$<1.0$	0.1
Insulin	$<1.0$	2.4
Feeding behaviour during the week of measurements		
Number of meals per day	8.9	8.7
Average daily feed intake	7.9	0.4
Total intake duration	6.2	< 1.0
Average meal size	3.5	9.8
Average meal duration	2.2	7.6

625 <sup>1</sup>The contribution of each variable is expressed as % of the variance (inertia) explained by each 626 component.

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628 **Table 5.** Characterization of groups after clustering according feeding behaviour, voluntary 629 test meal and pre-prandial plasma metabolites and insulin concentrations in growing pigs

	Clusters					P <sub>†</sub>	
	$\mathbf{1}$	$\overline{2}$	$\overline{3}$	$\overline{4}$	RSD <sup>+</sup>	$\mathsf{C}$	<b>BW</b>
Number of pigs fed LF-A0/LF-A2/LF-A4 diets	1/1/2	0/2/0	2/0/1	2/1/2			
Number of pigs fed HF-A0/HF-A2/HF-A4 diets	0/0/1	0/3/2	1/0/0	3/2/0			
Body weight (kg)	$34.9^{a}$	$37.5^{\overline{a}}$	$44.9^{\overline{b}}$	$43.0^{b}$	3.1	< 0.01	
Feeding behaviour							
Average daily feed intake (g DM/d)	$1209^{ab}$	$1174^{^a}$	$1580^{bc}$	$1838^\circ$	243	0.03	< 0.01
Number of meals per day	7.1 <sup>a</sup>	7.0 <sup>a</sup>	$11.0^{ab}$	$12.6^{b}$	3.2	0.04	0.71
Day of the blood kinetic							
Test meal size (g DM)	144 <sup>a</sup>	$242^a$	$223^{\degree}$	$462^b$	84	< 0.01	< 0.01
Interval since the last meal (min)	418	511	534	324	171	0.16	0.22
Pre-prandial plasmatic concentrations							
Insulin $(mUI/L)$ §	3.3	5.7	4.6	4.1	5.4	0.14	0.08
Glucose $(mg/L)$	1057	1034	1221	1174	97	0.14	0.51
Lactate $(\mu \text{mol/L})$	$989^{ab}$	$855^{\circ}$	$1139^{b}$	818 <sup>a</sup>	129	< 0.01	0.64
Free fatty acid (µmol/L)	290	95	118	91	150	0.17	0.27
Triglycerides (mg/L)	272	249	321	284	65	0.55	0.28
$\alpha$ -amino nitrogen (mg/L)	$516^a$	$645^{\mathrm{b}}$	$667^b$	$762^\circ$	56	< 0.01	0.80
Urea $(mg/L)$	$195^{\mathrm{b}}$	$112^a$	125 <sup>a</sup>	$172^b$	33	< 0.01	0.90

 $A0$ , no aleurone; A2, supplementation of 2 g/kg of aleurone; A4, supplementation of 4 g/kg of

631 aleurone; BW, body weight; C, cluster; DM, dry matter; HF, high fibre; LF, low fibre,

632 a,b,c Mean values within a column with unlike superscript letters were significantly different

633 (P<0.05).

634 † Analysis of variance performed using Proc Mixed (SAS) including effects of cluster (C) and

635 body weight (BW). Data are presented in table as least squares means (*lsmeans* statement in 636 SAS).

637 ‡ RSD= residual standard deviation.

638 § Logarithmic transformation was previously performed to validate normality test according

639 to Shapiro-Wilk's test of residual. Values are presented in table as means of the estimated

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640 data from MIXED model after exponential transformation. Residual standard deviation of 641 these variables is calculated as the standard error of the difference between experimental data 642 and estimated data.

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## **Figure legend**

 **Fig. 1.** Effect of dietary fibre and aleurone supplementation on plasma glucose (a, b), insulin 646 (c, d), lactate (e, f), free fatty acid (g, h), urea (i, j) and  $\alpha$ -amino-nitrogen (k, l) concentrations in growing pigs fed diets. Results are expressed as means, n=26. The experiment was conducted with 14 growing pigs fed LF diet, 12 growing pigs fed HF diet and with 9 growing pigs fed A0 diet, 9 growing pigs fed A2 diet and 8 growing pigs fed A4 diet. General linear mixed analysis was performed using MIXED model including the fixed effect of dietary fibre level, aleurone supplementation, interaction between dietary fibre and aleurone, time, interaction between time and dietary effect, size of the test meal, pre-prandial concentration of the metabolite or insulin and the random effect of batch. P-values are specified with their residual standard deviation (RSD) for the effects of dietary fibre level (a, c, e, g, i, k) and aleurone supplementation (b, d, f, h, j ,l). Interaction between DF level and aleurone supplementation was never significant. Effect of the time is significant for all metabolites and insulin concentrations except urea concentration. Interactions between time and dietary fibre 658 level or aleurone supplementation are not significant except for insulin and  $\alpha$ -amino-nitrogen. 659 \* Significant difference at that time between levels of fibre  $(C)$  or aleurone  $(D)$ ,  $P<0.05$ .

 **Fig. 2.** Effect of dietary fibre and aleurone supplementation on plasma triglyceride concentration in growing pigs fed experimental diets. Results are expressed as means, n=26. The experiment was conducted with 14 growing pigs fed LF diet, 12 growing pigs fed HF diet and with 9 growing pigs fed A0 diet, 9 growing pigs fed A2 diet and 8 growing pigs fed A4 diet. Analyse of variance was performed according a General linear mixed model using MIXED procedure of SAS including the fixed effect of dietary fibre level, aleurone supplementation, interaction between dietary fibre and aleurone, time, interaction between time and dietary effect, size of the test meal, pre-prandial concentration of the metabolite or insulin and the random effect of batch. P-values are specified with their residual standard 670 deviation (RSD) for the following effects: F: fibre, A: aleurone,  $Fx \cdot A$ : interaction between dietary fibre and aleurone. Effect of the time is significant (*P*<0.01) but interactions between time and dietary fibre level or aleurone supplementation are not significant.  $a,b,c$  significant dietary effect on mean triglycerides concentration during the hour after the test meal (*P*<0.05). 

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 **Fig. 3.** Effect of clustering according pre-prandial concentrations of plasma metabolites and insulin, feeding behaviour and size of the voluntary test meal on glucose (a), insulin (b), 677 lactate (c),  $\alpha$ -amino nitrogen (d), urea (e), free fatty acid (f) and triglyceride (g) concentrations in growing pigs. Results are expressed as means, n=26. The experiment was conducted with 5 growing pigs grouped in cluster 1, 7 growing grouped in cluster 2, 4 growing grouped in cluster 3 and 10 growing pigs grouped in cluster 4. General linear mixed analysis was performed using MIXED model including the fixed effects of cluster, time, their interaction and body weight and the random effect of batch. P-values are specified with their residual 683 standard deviation (RSD) for the effects clustering.  $a,b,c$ : significant effect of clustering on average metabolites concentrations during one hour after the test meal (*P*<0.05). Effect of the time is significant for all metabolites and insulin concentrations except urea concentration. Interactions between time and clustering are not significant except for triglycerides.

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**Fig. 2.** 

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