

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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18	
19	Abbreviations: ADFI: average daily feed intake; BW: body weight; CF: crude fibre; CP:
20	crude protein DE: digestible energy; DF: dietary fibre; DM: dry matter; EE: ether extract; HF:
21	high fibre; LF: low fibre; NDF: neutral detergent fibre; NE: net energy; ST: starch.
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35 Abstract

Variations in feeding behaviour between animals result from individual variations in their 36 metabolism as affected by diet composition. The study aimed to link the within-day dynamics 37 of voluntary feed intake and those of blood metabolites and insulin in growing pigs having ad 38 39 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 40 differing by fibre content (13 or 18% NDF) and aleurone supplementation (0, 2 or 4 g/kg). 41 Feeding behaviour was individually recorded during one week. The kinetic of plasma 42 metabolites and insulin was followed during 1 hour after a voluntary test meal. Dietary fibre 43 level did not affect daily feed intake but increased meal size and meal duration. Aleurone 44 supplementation (4 g/kg) decreased daily feed intake and number of meals. Dietary fibre level 45 only decreased insulin concentration measured 15 minutes after meal beginning. Aleurone 46 supplementation (4 g/kg) decreased glycaemia during the first hour after the meal and 47 insulinemia 15 minutes after the meal. Free access to feed led to high variability in pre-48 49 prandial metabolites and insulin concentrations resulting in different test meal size irrespective of diet composition. Animals were then spread over different profiles combining 50 feeding behaviour and fasted status to explain different profiles of regulation of feed intake. 51 Plasma metabolites and insulin kinetics were affected by diet composition but also by animal 52 characteristics. Individual variability should be considered when diet composition is used to 53 54 modulate feeding behaviour.

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Introduction 56

Dietary fibre (DF) modulates daily voluntary feed intake in association with changes in 57 feeding behaviour: number of meals, meal volume, meal duration and within day spreading of 58 meals ⁽¹⁾. In monogastric animals as pigs and humans, these effects may differ according to 59 60 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 61 average daily feed intake (ADFI), meal volume and feeding rate whereas inclusion of wheat 62 bran (NDF=23%) did not affect ADFI in pigs of 14 kg BW⁽²⁾. The impact of DF on satiety 63 can be explained either by 1.) dietary energy dilution, 2.) a direct effect due to the increase of 64 digestive content volume with activation of mechanoreceptors, 3.) an indirect effect via 65 metabolic regulation pathways, or 4.) fermentations with a production of short chain fatty 66 acids, as reviewed by Bach Knudsen⁽³⁾ and Li and Patience⁽⁴⁾. The variety of animal response 67 to the dietary inclusion of DF suggests that various hormonal, metabolic, physical and 68 microbial pathways are involved in the regulation of feed intake. Testing DF fractions is 69 needed to better distinguish the overall effect of DF on feed intake from the specific and 70 functional properties of some DF fractions ⁽³⁾. Wheat aleurone layer, a fraction of wheat bran 71 containing fibres (arabinoxylans and β -glucans) and phenolic compounds, ferulic acids and 72 lignans ⁽⁵⁾, is a suitable candidate as DF-source that can affect glucose and insulin 73 postprandial peaks as demonstrated in horses ⁽⁶⁾. 74

To our knowledge, few studies co-investigated the effect of DF level and the 75 supplementation of a particular fraction of DF on ADFI, feeding behaviour, plasma 76 metabolite and hormone kinetics. Therefore, this current study aimed to link the within-day 77 dynamics of voluntary feed intake, plasma metabolites, and insulin in growing pigs that had 78 79 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 80 modifies feeding behaviour in relation with changes in metabolites and insulin kinetics after a 81 meal, considering that feeding behaviour is closely linked with metabolite and insulin 82 variations⁽⁷⁾. 83

The implication of this study is the modulation of feeding behaviour in pigs. Limiting 84 voluntary feed intake by dietary composition rather than quantitative feed restriction may 85 benefit animal welfare and facilitate increased feed efficiency ⁽⁸⁾. Due to similitudes in 86 87 digestion and metabolism between pigs and humans, results obtained in this study also furnished hypotheses regarding human food intake regulation. 88

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Methods 89

The experiment was performed at the INRA experimental facilities in Saint-Gilles 90 (France) (agreement number: C35-275-32) in compliance with the French directive on animal 91 experimentation and care (2013-118) after evaluation by a competent ethical committee in 92 93 animal experimentation under the responsibility of the French ministry of research (authorization number 2016072907418869). 94

Animals, housing and experimental design 95

The experiment was conducted with forty castrated males ((Pietrain \times (Large White \times 96 Landrace)) with an average initial BW of 25.6 ± 3.0 kg (70 days of age). To avoid pain and 97 98 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 99 Melchior et al.⁽⁹⁾ under general anaesthesia (ketamine and isoflurane). After the surgery, pigs 100 101 had two weeks of recovery and adaptation to experimental diets and to individual housing. Then, pigs were weighed and individually housed in a metabolic cage (60×120 cm) with 102 metal floor placed in an enclosure (1.7 m^3) and equipped with a weighing scale in order to 103 continuously record feed consumption during seven days. The study was conducted during 104 thirteen batches of three or four littermates each. For each batch, the three or four littermates 105 with a similar BW were selected and successively housed during one week in the enclosure as 106 107 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 108 109 and one of the six experimental diets. During all the experiment, animals were carefully observed to detect potential injures of welfare and disease. 110

Experimental diets 111

112 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; 113 Minneapolis, Minnesota, United States of America; 0 g/kg: A0, 2 g/kg: A2 and 4 g/kg: A4) 114 were tested in six experimental diets (table 1). The HF diet contained a mixture composed of 115 50% of wheat bran, 33% of soya hulls and 17% of sugar beet pulp. This mixture of three DF-116 rich feedstuffs having different physicochemical properties permitted to study an overall 117 effect of DF level rather than the effect of DF from a specific source ⁽³⁾. Experimental diets 118 were balanced on the ratio of digestible lysine to net energy (NE). Energy content was lower 119 120 in the HF diets due to the introduction of DF (-6% of NE per kg of dry matter (DM) for HF diet ⁽¹⁰⁾). 121

Pigs received 500 g of a commercial growing feed (NDF=14%) on the first day after the 122 surgery, and then 1000 g per day during four days with a transition from the commercial diet 123 124 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 125 126 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 127 day. Each day, feed allowance was determined to be greater than voluntary daily feed intake. 128 To avoid feed spillage, feed was provided twice a day at 0845 and at 1645, before trough 129 emptying. The daily feed allowance was weighed and a sample of offered feed was cumulated 130 each day of measurements for each pig for immediate DM measurement. For each 131 experimental diet, samples were pooled over the whole experiment for chemical analyses. 132 Feed refusals and spillages were collected at the end of each week of measurements and were 133 oven-dried to determine the refused DM. 134

Feeding behaviour recording 135

136 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 137 began at 0900 and finished at 0600. For water intake calculations, a day of measurement 138 began at 0900 and finished at 0800 to take into account water meals when the feed trough was 139 140 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. 141 The weight of the feed trough and the water pit was recorded every 10 seconds. A 142 consumption of feed was defined as a negative variation of the weight of the feed trough. The 143 feed intake size was calculated as the difference between the stabilized weight of the trough 144 145 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 146 147 studies, successive feed bouts were grouped into the same meal using a meal criterion defined as the maximum length between two feed bouts owing to the same meal ⁽¹¹⁾. Feed bouts 148 separated by intervals shorter than the meal criterion were considered to be part of the same 149 meal and were clustered accordingly. The size of a meal was the sum of the size of the feed 150 bouts and the duration of the meal was the duration between the beginning of the first feed 151 bout and the end of the last feed bout of the meal. In our study, the meal criterion was 152 estimated using the log curves technique ⁽¹²⁾ and was established at four minutes. The DM 153 feed intake per meal was calculated as the feed intake per meal adjusted for the percentage of 154

DM of the feed measured weekly for each pig. Meals with a size below 10 g were not kept for 155 statistical analysis but spread over other meals of the day. The ADFI, expressed in g of DM 156 per day, was calculated for each pig as the average of dried feed intake from the 6 days 157 considered in the analysis. From the generated database, daily number of meals, average feed 158 159 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 160 behaviour. Daily total water intake was calculated as the difference of the water container 161 weight during 23-h periods. 162

Blood collection 163

On day 7, blood was sampled to analyse metabolites and insulin plasmatic concentrations. 164 The catheter was externalized outside of the enclosure and permitted to collect blood samples 165 without disturbing the animal. The first meal of day 7 was considered as a test meal. Blood 166 (10 mL) was sampled at 0830 and 0845 (referred as pre-prandial), at the beginning of the 167 meal and 15, 30, 45, 60 minutes after the beginning of the meal. Blood samples (10 mL per 168 169 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 170 -20°C until metabolites and hormone concentration analyses. For each blood sampling, the 171 haematocrit (H) was measured and a basal haematocrit (BH) was calculated as the mean of 172 pre-prandial haematocrits of this pig. Plasma metabolite and insulin concentrations were 173 adjusted as follows to take into account possible dilution because of water intake and saline 174 solution perfusion to flush the catheter line between successive samplings: 175

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

Chemical analyses 176

The experimental diets were analyzed for DM, ash, gross energy, nitrogen, ether extract, 177 crude fibre, different fibre fractions (NDF, ADF, ADL) and starch according to standard 178 procedures ⁽¹³⁾. Commercial kits were used to determine plasma concentrations of glucose 179 (Glucose RTU; bioMérieux, Craponne, France), lactate (Lactate PAP; bioMérieux, Craponne, 180 France), free fatty acids (NEFA-HR(2); Wako Chemicals GmbH, Neuss, Germany), urea 181 (Urea UV 250; bioMérieux, Craponne, France), α-amino nitrogen (Protéines-kit; bioMérieux, 182 183 Craponne, France) and triglycerides (Triglycérides Enzymatique PAP 150; bioMérieux, Craponne, France). These parameters were measured with a Konelab 20i device (Thermo 184

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Fisher Scientific, Courtaboeuf, France) according to manufacturers' recommendations. 185 Plasma concentrations of insulin were measured using an RIA kit (INSULIN-CT; CisBio 186 187 Bioassays, Codolet, France). Intra-assay CV was less than 5%.

Data analyses 188

189 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 190 Ether Extract, ST for Starch, CP for Crude Protein and CF for Crude Fibre ⁽¹⁰⁾ 191

Based on feeding behavior, between four to eight animals per treatment are necessary to 192 achieve the statistical power of 90% with an alpha level at 5% to see a difference of 100 g on 193 ADFI and a difference of 2 meals per day. 194

Pigs were individually housed in an enclosure. A batch was constituted by 3 or 4 195 littermates that were successively measured during one week each. One level of DF and three 196 levels of aleurone supplementation were tested during one batch and the other level of DF 197 (with its three levels of aleurone supplementation) was tested during the following batch. For 198 199 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. 200

The analysis thereafter was conducted using linear mixed model with the MIXED 201 procedure of SAS (SAS Inst. Inc., Cary, NC) and the assessment of significance of the factors 202 tested in each model was based on "Type 3 tests of fixed effects" as experimental design is 203 not strictly balanced. For variables considered as repeated effect, the REPEATED statement 204 was used in the procedure. An unstructured covariance matrix (type = UN) was used for these 205 models, because it was the covariance structure that displayed the lowest AIC and BIC in 206 comparison with other covariance structure that were tested (compound symmetry, Toeplitz 207 208 or autoregressive). Data were tested for normality according to Shapiro-Wilk's test of residual. 209

Variables describing feeding behaviour (ADFI, NE intake, number of meals, meal size, 210 meal duration and average interval between two meals) were analysed in a linear mixed 211 model with levels of DF, levels of aleurone and their interaction considered as main factors, 212 batch as a random factor and day of the week as a repeated effect with the pig as the 213 experimental unit. 214

Water intake per day was analysed in a linear mixed model with levels of DF, levels of 215 216 aleurone and their interaction considered as main factors, feed intake level and number of

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

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

Pre-prandial plasmatic concentration of metabolites (glucose, lactate, free fatty acids, 222 triglycerides, urea and α -amino nitrogen) and insulin were analysed in a linear mixed model 223 with levels of DF, levels of aleurone and their interaction considered as main factors, the 224 interval since the last meal and the size of this last meal as covariates, batch as a random 225 factor and time as a repeated effect with the pig as the experimental unit. 226

227 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 228 of this test meal (expressed as g/kg BW^{0.60}) and pre-prandial concentration of analysed 229 metabolites as covariates, batch as a random factor and time as a repeated effect with the pig 230 231 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 232 pairwise comparison of the means for each time. LS-means were calculated to obtain adjusted 233 means from the statistical model. When data are unbalanced, LS-means give better mean 234 estimates than simple means (LSMEANS statement in SAS). 235

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

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Data for pre-meal insulin concentration and concentrations of glucose, insulin, urea, free 249 fatty acids and triglycerides during the hour after the test meal were log-transformed before 250 251 statistical analyses.

Differences between treatments were considered significant for P < 0.05 whereas 252 253 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. 254

Results 255

Two pigs fed the LF-A0 and HF-A4 diets exhibited fever associated with a low ADFI on 256 the week of measurements. They were excluded from the experiment and subjected to 257 antibiotic treatments (150 mg Amoxicillin per 10 kg for BW). Consequently, 38 pigs were 258 considered in the final analysis. Only the data from 26 pigs that were fed two voluntary meals 259 between 0900 and 1700 on the day of blood kinetic were considered in the statistical analysis 260 of plasma metabolites and insulin concentrations. 261

262

Influence of diets on feeding behaviour.

263 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%, 264 P < 0.01) meals with high level of DF, without effect on ADFI and NE intake (table 2). 265 Whereas average meal duration (+10%, P < 0.01) and interval between two meals increased 266 (+14%, P<0.01) with DF level, the total daily feed intake duration was similar. The decrease 267 in ADFI (-20%, when compared with other diets; P < 0.01) for aleurone supplementing diet (4 268 g/kg) was associated with a decreased number of meals per day (P < 0.01). Pigs spent less time 269 per day to eat and interval between two meals was extended (P < 0.01) with diets 270 supplemented with 4 g/kg of aleurone. Neither DF level nor aleurone supplementation 271 272 modified total water intake, considering feed intake and number of meals as covariates.

Influence of diets on plasmatic metabolites and insulin concentrations. 273

There was no interaction between DF level and aleurone supplementation on pre-prandial 274 plasmatic concentration of metabolites and insulin. High level of DF decreased pre-prandial 275 insulin concentration (P=0.01) and tended to decrease pre-prandial glucose concentration 276 (P=0.06) when compared with the diets with low level of DF (table 3). The pre-prandial 277 insulin concentration was the greatest with aleurone supplemented diet at 2 g/kg compared to 278 others aleurone supplementations (P < 0.01). The pre-prandial α -amino-nitrogen concentration 279 280 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 281

increase of the interval between the test-meal and the last meal decreased pre-prandial 282 concentration of insulin (P<0.01) and increased pre-prandial free fatty acids concentration 283 284 (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). 285

286 The size of the voluntary test meal was greater with high level of DF (368 vs 242 g of DM, P=0.04) and longer (19.4 min. vs 13.8 min., P=0.02). It was not modified with aleurone 287 supplementation (data not shown). Except for urea concentration (P=0.18), concentrations of 288 all metabolites and insulin significantly changed during the first hour after the test meal 289 (P < 0.01, figure 1). During the first hour, there was no interaction between DF level and 290 aleurone supplementation for α -amino-nitrogen, urea, free fatty acids and insulin 291 292 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 293 (P=0.02; figure 2). Dietary fibre level did not affect any kinetics of metabolites and insulin 294 throughout the first postprandial hour whereas aleurone supplementation decreased glycemia 295 296 (P < 0.01; figure 1(b)). Insulin concentration at 15 minutes after the meal was lower for pigs fed high level of DF (P=0.03) and was lower for pigs fed aleurone supplemented diet (4 g/kg) 297 than pigs fed diet without aleurone supplementation (P=0.04). 298

299

Characterization of clusters.

Two principal components accounting for 49% of total variance among pigs were retained 300 from the multiple factorial analyses with 30% for the first component and 19% for the second 301 component. Contributions of each variable to these two major components are presented in 302 table 4. Based on the multiple factorial analyses, the hierarchical classification discriminated 303 pigs according to four clusters. Dietary treatment only partially agreed with cluster 304 305 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 306 307 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. 308 Additionally, pigs grouped in cluster 4 ate a more important voluntary test meal than those 309 grouped in other clusters (P < 0.01). Pre-prandial plasma concentration of free fatty acids was 310 greater for pigs in clusters 1 and 3 than for pigs in clusters 2 and 4 (P<0.01). Pre-prandial α -311 amino-nitrogen concentration varied from 516 mg/L for pigs from cluster 1 to 762 mg/L for 312 313 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). 314

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During the first hour after the meal, glucose, lactate, triglycerides and insulin kinetics did 315 not differ between clusters whereas free fatty acids, α -amino nitrogen and urea concentrations 316 were affected (figure 3). Free fatty acids concentration was greater for pigs grouped in 317 clusters 1 and 3 than for pigs grouped in clusters 2 and 4 (P<0.01; figure 3(d)). Concentration 318 319 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 320 grouped in clusters 2 and 3 (*P*<0.01; figure 3(f)). 321

Discussion 322

Dietary fibre level or aleurone supplementation modified feeding behaviour and blood and 323 insulin kinetics in pigs having free access to feed during 20.5 hours per day. No interaction 324 325 between DF level and aleurone supplementation was found. Dietary fibre level did not affect ADFI but increased meal size (+ 28 g) and meal duration (+ 1 min) while reducing the 326 327 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 328 329 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 330 affect feeding behaviour. 331

In pigs fed diets enriched in DF diluting energy concentration (-25% of digestible energy), 332 regulations of voluntary feed intake often lead to increased ADFI (+850 g of DM) to satisfy 333 energy requirements ⁽¹⁶⁾. In our study, DF enrichment, diluting the NE concentration by only 334 6% when compared with the control diet, did not reduce ADFI. Similarly, a NE dilution of 335 5% did not modify feed intake in growing pigs between 35 and 50 kg of BW ⁽¹⁷⁾. 336 Nevertheless, HF diet modified feeding behaviour, with pigs eating fewer meals per day of 337 338 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 339 delay the initiation of the next meal ⁽¹⁸⁾. This delay could be due to the production of short 340 chain fatty acids by microbial bacteria, using DF as substrates for fermentation ⁽¹⁹⁾. Meal size 341 is partly regulated by activation of mechanoreceptors and the distension of the stomach 342 leading to an early volumetric satiety ⁽²⁰⁾. With the HF diet and its bulking properties, meals 343 were expected to end sooner, resulting in smaller meal size due to an earlier stimulation of 344 mechanoreceptors after meal onset. In our study, greater meals suggest that this regulation 345 346 pathway was not enhanced with HF diet compared with LF diet and a possible adaptation of stomach to counteract the physical volumetric effect of DF⁽²¹⁾. Physical effects of DF on meal 347

size depend on the introduction rate and nature of fibrous sources, on the BW of the pig, and 348 on the duration of the adaptation period to the DF-rich diet ^(2; 22). In the present study, a 349 mixture of three DF sources (wheat bran, sugar beet pulp and soya bean hulls) with different 350 physical properties was used to test an overall DF effect rather than the consequences of a 351 specific property ⁽²²⁾. In addition, the BW of pigs (37 kg) and the adaptation period (2 weeks) 352 were probably sufficient to satisfactorily adapt the digestive tract of the pigs with an increase 353 of the empty stomach weight (276 g vs 293 g for LF and HF diets respectively, P<0.01, data 354 not shown). Moreover, meal size and duration are also regulated by metabolite concentrations 355 as suggested by the glucostatic theory of feed intake regulation ⁽²³⁾. In our study, this 356 metabolic regulation could be more important than bulking effect of high DF level. With DF 357 358 level, longer (+ 1 min) and greater (+28 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 359 HF diets respectively), although glycaemia did not significantly differ between HF and LF 360 diets (1112 and 1050 mg/L for pigs fed LF and HF diet respectively, as predicted from the 361 362 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 363 study, the three fibre sources used in the HF diets are known to delay gastric emptying and to 364 reduce digestibility of starch sources ⁽²⁴⁾. Increased duration of meals may thus permit to pigs 365 to reach glucose homeostasis. The delayed end of the meal may be due to the lower 366 concentration of insulin with DF level, which underlines the importance of some hormones in 367 regulation of feed intake. 368

The decrease in NE intake with aleurone supplementation (4 g/kg) suggested that 369 regulations of ADFI did not result in a constant intake of NE in all cases. The decreased ADFI 370 was explained by a decreased meal number without increase of meal size. This result suggests 371 an extension of satiety which could be partially explained by microbial activity ⁽²⁵⁾. In our 372 373 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 374 fatty acid concentrations with a possible inhibition of hormone-sensitive lipase ⁽²⁶⁾. As 375 suggested in previous studies in pigs ⁽²⁷⁾ and rats ⁽²⁸⁾, wheat aleurone-rich flour increased short 376 377 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 378 maintenance requirements ⁽²⁹⁾) and they can modify long term energy homeostasis ⁽³⁰⁾. Short 379 chain fatty acids stimulate satiety hormones like GLP-1 or PYY, thus inhibiting the initiation 380

of a next meal ^(31; 32). Satiety can also be linked to a period of elimination of metabolic waste 381 resulting from hepatic oxidation and nitrogen metabolism ⁽³³⁾. Regulation of metabolic waste 382 elimination occurs probably more than one hour after the meal. Because urea concentration 383 did not differ between treatments, the present results did not support this hypothesis. The 384 385 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 386 387 and wheat bran.

The different pathways permitting the regulation of feed intake (digestive, hormonal, 388 metabolic or microbial) coexist but their relative importance at a specific time might depends 389 on diet composition (DF, aleurone) and animal characteristics. In our trial, as pigs had free 390 391 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 392 ranged from 69 g to 379 g DM ingested per meal. In most of the experiments studying 393 metabolite or hormone kinetics, animals were fasted during at least 12 hours before receiving 394 a test-meal of a fixed amount ⁽³⁴⁾ whereas in commercial farms, pigs do not have similar ADFI 395 or feeding behaviour. Consequently, it is needed to let pigs eat with constraints as limited as 396 possible to assess the importance of each regulation mechanism behind this variability to 397 optimize nutritional solution. On the day of blood kinetics measurements, the interval 398 between the meal preceding the test meal and the test meal varied from 115 to 911 minutes. 399 The size of this last meal varied from 21 to 385 g of DM. Pigs did not have the same 400 metabolic status at the beginning of the kinetic measurements. Pre-prandial glycaemia ranged 401 from 689 to 1201 mg/L and pre-prandial free fatty acids concentration ranged from 45 to 402 485 µmol/L. Moreover, as the test meal was a voluntary meal, its size was extremely variable 403 404 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 405 406 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 407 408 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 409 ingestion of the meal test and fitted to metabolic responses of control groups in other studies 410 ^(7; 35). These animals had almost 9 hours of fasting before the beginning of the kinetic 411 412 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 413

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aleurone supplementing diets. The low level of free fatty acids during the first hour after the 414 meal might be explained with the low pre-prandial concentration of free fatty acid and with 415 the production of short chain fatty acids which are known to decrease free fatty acids 416 plasmatic concentrations ⁽²⁶⁾. This underlines the importance of microbial activity in changes 417 of feeding behaviour due to DF level. An increase of meal frequency (cluster 4) induced 418 changes of regulation pathways of feed intake. In this cluster, pigs fed different experimental 419 diets suggesting that animal characteristics could be more important than diet composition in 420 some post-prandial responses. This result is in accordance with another study which showed 421 an important variability of feeding behaviour in the same group ⁽³⁶⁾. Despite a low level of 422 plasma free fatty acids, these pigs had a heavier test meal than pigs of the other clusters, 423 424 which might be due to the heavy BW of animal suggesting a larger stomach and ingestion capacity. The large meal size was associated with a high concentration of α -amino nitrogen 425 whereas glucose and insulin responses were less modified. Although not significant, our 426 results are in accordance with others studies that exhibited less daily fluctuations of glucose 427 and insulin with increased meal frequency ^(7; 37). Other studies reported that kinetics on 428 glucose did not only depend on diet composition but also of feeding behaviour ⁽³⁸⁾. We 429 supposed that frequent meals induced a continuous supply of glucose and other nutrients 430 without important fluctuations of their plasmatic concentration. Glucose metabolism may not 431 be the first regulation pathway which modulates feed intake in these pigs. Finally, whereas 432 others clusters showed a large test meal size (> 220 g) compared with average meal size over 433 the measurement period (< 200 g), pigs grouped in cluster 1, fed predominantly LF diet, 434 showed a test meal more representative of the averaged meal size over other days. As pigs 435 belonging to this cluster were light (34.9 kg), their ingestion capacity may be limited. Due to 436 437 the small meal size, pigs presented a low α -amino-nitrogen concentration associated with high urea concentrations in pre-prandial situation and one hour after the meal. These results 438 439 suggest that pigs mobilized protein storages to meet energy requirements.

To conclude, there was no interaction between DF level and aleurone supplementation on 440 feeding behaviour in growing pigs. Dietary fibre level in the diet increased meal size and 441 decreased daily meal number without affecting ADFI whereas aleurone supplementation 442 decreased ADFI with a reduction of the meal number per day. The dietary supplementation 443 with wheat aleurone modulated feed intake with effect of satiety regulation pathways, when 444 445 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 446

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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.

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461 **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.

469 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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https://www.bahubburg.angl.or/kenks/https://katugn.afbf?/k0097if45f800378 plasma energy metabolites and insulin l 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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	I	low Fib	re	High Fibre				
	A0	A2	A4	A0	A2	A4		
Ingredients (g/kg of DM)								

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

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	Wheat	339.6	339.6	339.6	219.7	219.7	219.7
	Corn	219.7	219.7	21.97	219.7	219.7	219.7
	Barley	219.7	219.7	21.97	219.7	219.7	219.7
	Soybean meal	185.9	185.9	185.9	157.5	157.5	157.5
	Rapeseed oil	5.0	5.0	5.0	5.0	5.0	5.0
	Wheat bran	-	-	-	75.0	75.0	75.0
	Soya hulls	-	-	-	50.0	50.0	50.0
	Sugar beet pulp	-	-	-	25.0	25.0	25.0
	Aleurone ⁺	-	2.0	4.0	-	2.0	4.0
	Premix ‡	30.0	29.8	29.6	28.3	28.1	27.9
Chem	ical composition						
Analy	sed (% DM or precised)						
	Crude protein	18.1	18.3	18.0	16.8	17.7	17.8
	Crude fat	3.6	3.3	3.5	3.5	3.5	3.2
	Crude fibre	2.6	2.8	2.8	4.8	5.1	5.0
	NDF	10.1	10.6	10.4	14.5	14.6	14.9
	ADF	3.3	3.5	3.3	5.8	5.8	5.9
	ADL	0.5	0.6	0.6	0.9	0.9	0.7
	Starch	56.7	53.7	53.4	49.9	47.5	48.2
	Gross energy (MJ/kg DM)	18.38	18.24	18.18	18.12	18.20	18.07
Measu	ared (MJ/kg DM)						
	Digestible energy	16.21	15.80	15.80	15.06	15.02	15.73
	Metabolisable energy	15.87	15.37	15.43	14.78	14.66	15.33
Calcul	lated (MJ/kg DM) §						
	Net energy	11.32	11.14	11.10	10.53	10.57	10.47
1.0	1 10 1		/1 C	1			0.4 //

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

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

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
- 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;

- 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;
- pantothenic acid, 2000 mg; vitamin B6, 1 mg; vitamin B12, 0.022 mg; niacinamide, 15 mg;
- 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= $0.703 \times DE + 1.58 \times CF + 0.47 \times ST$ -
- 582 0.97×CP-0.98×CF⁽⁹⁾ with DE for Digestible Energy, EE for Ether Extract, ST for Starch, CP
- 583 for Crude Protein and CF for Crude Fibre ⁽⁹⁾

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584	Table 2.	Effect	of	dietary	fibre	and	aleurone	supplementation	on	feeding	and	drinking
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	Fibre			A	Aleuror	ie		Р	†
	LF	HF		A0	A2	A4	-		
Number of pigs	18	20	•	13	14	11	RSD‡	F	А
Body weight (kg)	37.2	37.8	-	38.0	37.6	36.8	4.0	0.69	0.68
Average daily feed intake (g DM/day)	1420	1445		1562 ^a	1487 ^a	1248 ^b	334	0.73	< 0.01
Net energy intake per day (kJ NE/kg BW ^{0.60} /day)§	1684	1777		1900	1667	1581	266	0.35	0.05
Number of meals per day §	9.4	8.2		9.1 ^a	9.4 ^a	7.6 ^b	3.2	< 0.01	< 0.01
Average feed intake per meal (g DM/meal) §	149	177		173	153	167	48	< 0.01	0.40
Average meal duration (min) §	9.9	10.9		10.2	10.2	10.9	3.7	< 0.01	0.16
Total meal duration per day (min/day) §	90	87		90 ^a	92 ^a	81 ^b	25	0.17	0.01
Interval between two meals (min) §	145	166		150 ^a	144 ^a	176 ^b	55	< 0.01	< 0.01
Water intake (g/day) §	2973	3074		2926	3123	3013	1547	0.88	0.89

585 behaviour in growing pigs

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

The experiment was conducted with 5 growing pigs fed LF-A0, 7 growing pigs fed LF-A2, 6 growing pigs fed LF-A4, 8 growing pigs fed HF-A0, 7 growing pigs fed HF-A2 and 5 growing pigs fed HF-A4.

^{a,b} Mean values within a column with unlike superscript letters were significantly different (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
SAS).

597 **‡** RSD= residual standard deviation.

§ Logarithmic transformation was previously performed to validate normality test accordingto 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

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

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

	Fil	bre	Aleurone			<i>P</i> †				
	LF	HF	A0	A2	A4	-				
Number of pigs	14	12	9	9	8	RSD¶	F	А	Ι	LMS
Insulin (mUI/L) §	5.8	3.1	3.7 ^a	6.7 ^b	3.0 ^a	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 (µmol/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
α-amino nitrogen										
(mg/L)	645	671	697 ^a	701 ^a	576 ^b	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
aleurone; DM, dry matter; HF, high fibre; LF, low fibre

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 growing pigs fed HF-A4.

^{a,b} Mean values within a column with unlike superscript letters were significantly different
 (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

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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- these variables is calculated as the standard error of the difference between experimental data 620
- and estimated data. 621

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Table 4. Contributions¹ of each variable to components 1 and 2 in the Multiple Factorial 622 Analysis performed on pre-prandial plasmatic metabolite and insulin concentrations and 623 feeding behaviour in growing pigs 624

	Component 1	Component 2
Voluntary meal size	36.3	11.9
Pre-prandial plasmatic concentration		
α-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 ¹The contribution of each variable is expressed as % of the variance (inertia) explained by each 626 component.

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

		Clu	sters			Р	†
	1	2	3	4	RSD‡	С	BW
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 ^a	44.9 ^b	43.0 ^b	3.1	< 0.01	-
Feeding behaviour							
Average daily feed intake (g DM/d)	1209 ^{ab}	1174 ^a	1580 ^{bc}	1838 [°]	243	0.03	< 0.01
Number of meals per day	7.1 ^a	7.0 ^a	11.0 ^{ab}	12.6 ^b	3.2	0.04	0.71
Day of the blood kinetic							
Test meal size (g DM)	144^{a}	242 ^a	223 ^a	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 (µmol/L)	989 ^{ab}	855 [°]	1139 ^b	818 ^a	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
α-amino nitrogen (mg/L)	516 ^a	645 ^b	667 ^b	762 [°]	56	< 0.01	0.80
Urea (mg/L)	195 ^b	112 ^a	125 ^a	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

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

^{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

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

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

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644 **Figure legend**

Fig. 1. Effect of dietary fibre and aleurone supplementation on plasma glucose (a, b), insulin 645 (c, d), lactate (e, f), free fatty acid (g, h), urea (i, j) and α -amino-nitrogen (k, l) concentrations 646 in growing pigs fed diets. Results are expressed as means, n=26. The experiment was 647 648 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 649 mixed analysis was performed using MIXED model including the fixed effect of dietary fibre 650 level, aleurone supplementation, interaction between dietary fibre and aleurone, time, 651 652 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 653 654 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 655 supplementation was never significant. Effect of the time is significant for all metabolites and 656 insulin concentrations except urea concentration. Interactions between time and dietary fibre 657 658 level or aleurone supplementation are not significant except for insulin and α -amino-nitrogen. * Significant difference at that time between levels of fibre (C) or aleurone (D), P < 0.05. 659

Fig. 2. Effect of dietary fibre and aleurone supplementation on plasma triglyceride 661 concentration in growing pigs fed experimental diets. Results are expressed as means, n=26. 662 The experiment was conducted with 14 growing pigs fed LF diet, 12 growing pigs fed HF diet 663 and with 9 growing pigs fed A0 diet, 9 growing pigs fed A2 diet and 8 growing pigs fed A4 664 diet. Analyse of variance was performed according a General linear mixed model using 665 MIXED procedure of SAS including the fixed effect of dietary fibre level, aleurone 666 667 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 668 insulin and the random effect of batch. P-values are specified with their residual standard 669 deviation (RSD) for the following effects: F: fibre, A: aleurone, $F \times A$: interaction between 670 671 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 672 dietary effect on mean triglycerides concentration during the hour after the test meal (P < 0.05). 673 674

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Fig. 3. Effect of clustering according pre-prandial concentrations of plasma metabolites and 675 insulin, feeding behaviour and size of the voluntary test meal on glucose (a), insulin (b), 676 lactate (c), α -amino nitrogen (d), urea (e), free fatty acid (f) and triglyceride (g) concentrations 677 in growing pigs. Results are expressed as means, n=26. The experiment was conducted with 5 678 679 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 680 performed using MIXED model including the fixed effects of cluster, time, their interaction 681 and body weight and the random effect of batch. P-values are specified with their residual 682 standard deviation (RSD) for the effects clustering. ^{a,b,c}: significant effect of clustering on 683 average metabolites concentrations during one hour after the test meal (P < 0.05). Effect of the 684 time is significant for all metabolites and insulin concentrations except urea concentration. 685 Interactions between time and clustering are not significant except for triglycerides. 686

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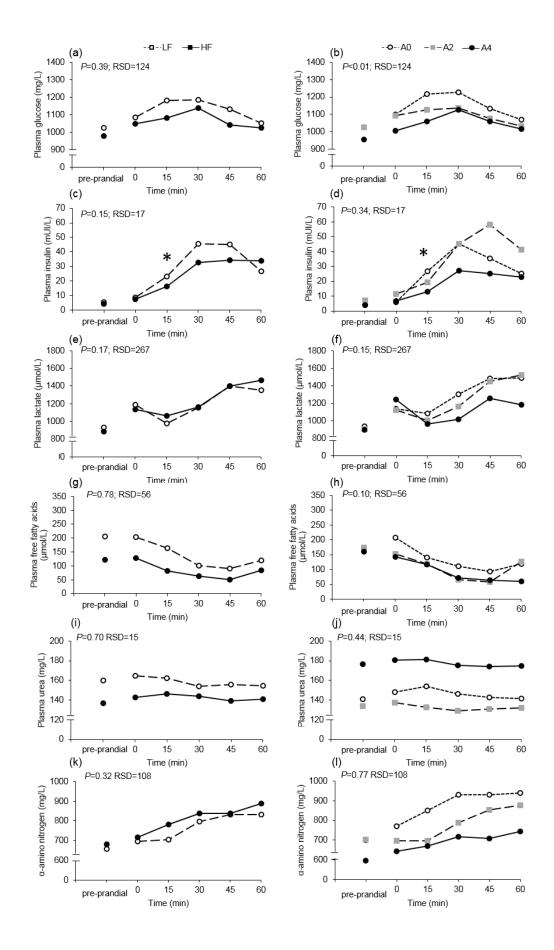


Fig. 1.

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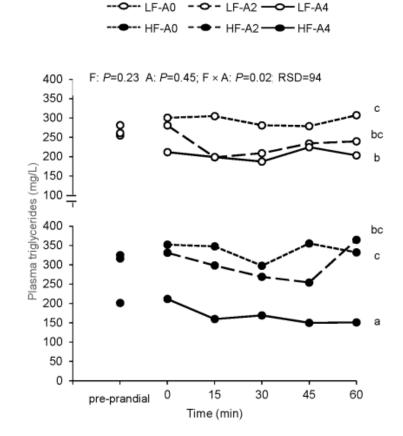


Fig. 2.

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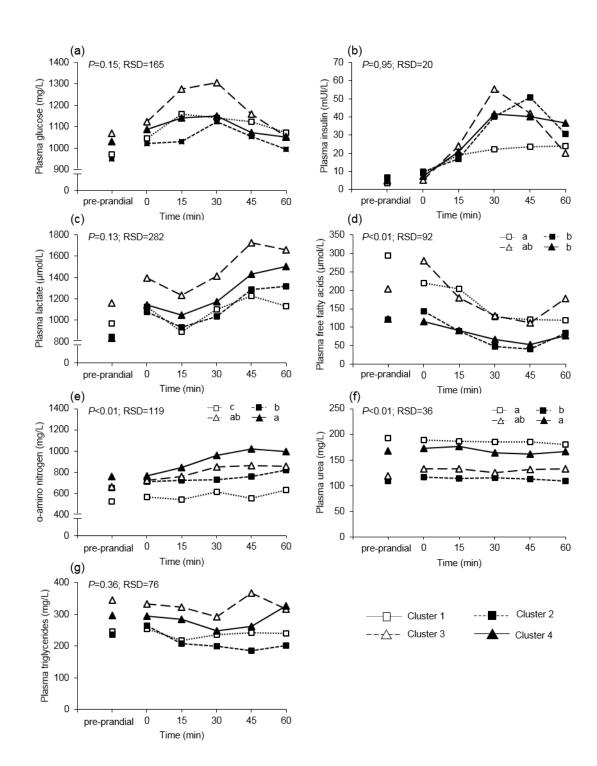


Fig. 3.

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