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SHORT COMMUNICATION

A combined pig model to determine the net absorption of volatile fatty acids in the large intestine under different levels of crude fiber

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Abstract

Background: This study aimed to develop a combined model to quantify the net absorption of volatile fatty acids (VFA) in the large intestine (LI) of pigs.

Methods: Fifteen female growing pigs (Duroc × Large White × Landrace) were ranked by body weight (30 ± 2.1 kg) on day 0 and assigned to one of three treatments, namely the basal diet containing different crude fiber (CF) levels (LCF: 3.0% CF, MCF: 4.5% CF, and HCF: 6.0% CF). The pigs were implanted with the terminal ileum fistula and the cannulation of the ileal mesenteric vein (IMV), portal vein (PV), and left femoral artery (LFA) from days 6 to 7. [^{13}C]-Labeled VFA and P-aminohippuric acid were constantly perfused into the terminal ileum fistula and the cannulation of the IMV (day 15), respectively. Blood samples were collected from the PV and the LFA during perfusion (5 h), and LI samples were collected.

Results: The net flux of [^{12}C]-acetic acid in the PV was greater for LCF versus MCF ($p = 0.045$), but no difference was observed in the net flux of [^{12}C]-propionic acid ($p = 0.505$) and [^{12}C]-butyric acid ($p = 0.35$) in the PV among treatments. The deposition of [^{12}C]-acetic acid in the LI was greater for LCF versus MCF ($p = 0.014$), whereas the deposition of [^{12}C]-propionic acid ($p = 0.007$) and [^{12}C]-butyric acid ($p = 0.037$) in the LI was greater for LCF versus HCF.

Conclusions: In conclusion, this pig model was found conducive to study the net absorption of VFAs in the LI, and LCF had more net absorption of VFAs in the LI than MCF and HCF.

KEYWORDS
crude fiber, growing pigs, large intestine, T-type fistula, volatile fatty acids

1 | INTRODUCTION

Fermentation of a series of carbohydrates occurs in the cecum and colon of animals by anaerobic microorganisms, with organic acids and gases derived as major end products.[1–3] The yield and pattern of volatile fatty acids (VFA) in the large intestine (LI) may be changed by the number and species of microorganisms, which can be affected by fermented substrates.[4] For single-stomach species (e.g., pigs and humans), microbial fermentation of nutrients in the LI produces VFAs, and lactic acids are efficiently absorbed in the cecum and colon. VFAs absorbed in the LI are estimated to meet about 5%–28% of energy maintenance needs for pigs.[5–7] VFA produced as a result of fermentation by bacterial flora in the LI, especially in the cecum, was beneficial to the health of the intestine and the host animal itself.[3] Besides, appropriately increasing dietary fiber levels could reduce the feed cost for pig breeding and benefit pigs' health and physical condition.[8] All these factors show that the quantitative determination of VFA absorption in the LI is meaningful.

The different dietary levels of crude fiber (CF; 6.7% CF vs. 9.5% CF) would affect the production and absorption of VFAs in the LI, especially acetic acid.[1] Additionally, there were significant changes in the production rates of VFAs for pigs fed diets with different CF levels.[7] Dietary CF content plays a vital role in the production of VFA and gut health.[9] The absorption of VFAs in the gastrointestinal tract (GIT) has been studied by collecting blood from the veins of the stomach, small intestine, and LI.[10] Furthermore, the blood vessel cannulation model has been used to explore the effect of starch sources on the net portal flux of glucose, VFAs, and amino acids in pigs.[11] Using a similar procedure, a research study evaluated the net flux of nutrients across portal-drained viscera in lactating dairy cows.[12] These aforementioned studies showed that blood vessel cannulation had been widely applied to the study of enteral nutrient metabolism. However, conventional methods do not distinguish between endogenous and exogenous nutrients. Endogenous nutrients are difficult to dynamically track based on metabolic changes because the whole digestive tract of animals is indivisible before slaughter and dissection. It was noted that the daily VFA absorption rates from the whole LI calculated by subtracting the daily fecal excretion of VFAs from the estimated daily VFA production rates using traditional measurement were approximate, and more precise studies were needed.[1] Based on these concerns, our group used a combined model of pigs in this study to determine the net absorption of VFAs in the LI accurately. We established an ileum fistula operation to eliminate the interference of the anterior GIT in the LI. And by collecting blood samples simultaneously from the portal vein (PV) and left femoral artery (LFA), the net absorption of VFAs in the PV per unit of time can be estimated.[13] Meanwhile, there was no difference in the absorption of VFAs with different carbon isotopes in the GIT,[14] so the isotopic tracer method was used to quantify the endogenous nutrients in LI accurately.

Thus, we hypothesized that this combined pig model could accurately quantify the endogenous nutrients in the LI. Therefore, the present study was conducted to determine the effects of dietary CF levels on the net absorption of VFAs in the LI using [^{13}C]-labeled VFA perfusion and gas chromatography–mass spectrometry (GC–MS) analysis of VFA levels in the blood and LI.

2 | MATERIALS AND METHODS

2.1 | Animal ethics

All pigs used here were selected from the Hubei Academy of Agricultural Sciences in Wuhan City. The experiment and animal handling procedures were approved by the Animal Care and Use Committee of Wuhan Polytechnic University (2010–0029).

Specific detailed materials and methods are available in the Supporting information, the main contents of which include the following:

2.2 | Animals and experimental treatments[15]

2.3 | The surgical procedure of installing the cannulation

2.4 | Solution preparation and perfusion details[14]

2.5 | Sampling[16]

2.6 | GC–MS analysis[17,18]

2.7 | The formula for calculation of relative indices[19,20]

2.8 | Statistical analysis

3 | RESULTS

3.1 | Blood flow rate of PV

No treatment effects were detected ($p = 0.162$) on the blood flow rate of the PV (Table 1).

3.2 | The net flux of acetic acid in the PV and the deposition of acetic acid in the LI

No treatment effect was detected ($p = 0.848$) for [^{12}C]-acetic acid concentrations in the PV (Table 2) and [12C]-acetic acid concentrations in the LFA ($p = 0.757$). However, both the net flux of [^{12}C]-acetic acid in the PV ($p = 0.045$) and the net flux of total acetic acid in the PV ($p = 0.035$) were greater for LCF (a basal diet of 3% crude fiber) compared with MCF (a basal diet of 4.5% crude fiber) but were similar for HCF (a basal diet of 6% crude fiber) compared with

LCF and MCF. No treatment effects were detected ($p=0.911$) for the net flux of [^{13}C]-labeled acetic acid in the PV as expected. The deposition of [^{12}C]-acetic acid in the LI ($p=0.014$), the deposition of [^{13}C]-labeled acetic acid in the LI ($p=0.045$). The net absorption of total acetic acid in the LI ($p=0.035$) was greater for LCF compared with that for MCF but was similar for HCF compared with LCF and MCF.

3.3 | The net flux of propionic acid in the PV and the deposition of propionic acid in the LI

Table 3 shows that no treatment effects were detected on concentrations of [^{12}C]-propionic acid in the PV ($p=0.199$), concentrations of [^{12}C]-propionic acid in the LFA ($p=0.873$), net flux of [^{12}C]-propionic acid in the PV ($p=0.505$), net flux of [^{13}C]-labeled propionic acid in the PV ($p=0.816$), and net flux of total propionic acid in the PV ($p=0.959$). Pigs assigned to HCF had reduced ($p=0.007$) deposition of [^{12}C]-propionic acid in the LI compared with LCF and MCF pigs. No treatment effects were detected ($p=0.248$) on deposition of [^{13}C]-labeled propionic acid in the LI. The net absorption of total propionic acid in the LI ($p=0.002$) was greater for LCF and MCF compared with HCF and was similar between LCF and MCF.

TABLE 1 Effect of the different levels of crude fiber supplementation on the blood flow rate of portal vein in growing pigs.

Item[1]	LCF	MCF	HCF	*p*-value
F (L/h)	7.38 ± 1.79	6.87 ± 1.14	10.25 ± 0.41	0.16

Note: Values are presented as means ± SEM, $n=5$ (1 pig/pen).

Abbreviations: *F*, blood flow rate of portal veins; SEC, standard error of the mean.

[1]LCF is a basal diet of 3% crude fiber; MCF is a basal diet of 4.5% crude fiber; HCF is a basal diet of 6% crude fiber.

3.4 | The net flux of butyric acid in the PV and the deposition of butyric acid in the LI

Table 4 shows that no treatment effects were detected on concentrations of [^{12}C]-propionic acid in the PV ($p=0.118$), concentrations of [^{12}C]-propionic acid in the LFA ($p=0.366$), net flux of [^{12}C]-propionic acid in the PV ($p=0.35$), net flux of [^{13}C]-labeled propionic acid in the PV ($p=0.599$), and net flux of total propionic acid in the PV ($p=0.478$). Deposition of [^{12}C]-butyric acid in the LI was greater ($p=0.037$) for LCF compared with HCF and was similar for MCF compared with LCF and HCF. Deposition of [^{13}C]-labeled butyric acid in the LI did not differ ($p=0.814$) for LCF, MCF, and HCF. Net absorption of total butyric acid in the LI was greater ($p=0.044$) for LCF compared with HCF and was similar for MCF compared with LCF and HCF.

4 | DISCUSSION

Exogenous and endogenous nutrients are the two sources of nutrients utilized by animals.[21] Exogenous nutrients (e.g., glucose and amino acids) can be absorbed by the body after the digestion of feed in the anterior GIT.[21,22] The microbial fermentation of nutrients produces endogenous nutrients (e.g., VFAs and lactic acids) in the LI that have not been digested and absorbed in the anterior GIT.[1,2] Acetic acid, propionic acid, and butyric acid function as energy providers and intestinal

TABLE 2 Effect of the different levels of crude fiber supplementation on the net flux of acetic acid in the portal vein and the deposition of acetic acid in the large intestine of growing pigs.

Item[1]	LCF	MCF	HCF	*p*-value
^{12}C-aaCp (mg/L)[2]	682.65 ± 130.20	729.35 ± 100.30	648.10 ± 52.70	0.85
^{12}C-aaCa (mg/L)[2]	567.10 ± 108.70	620.95 ± 72.20	541.30 ± 18.65	0.76
^{12}C-aaF$_{VFA}$ (mg/h)[3]	837.50 ± 69.17^{a}	487.92 ± 68.75^{b}	719.17 ± 165.42^{ab}	0.045
^{13}C-aaF$_{VFA}$ (mg/h)[3]	42.92 ± 16.25	36.25 ± 6.67	38.75 ± 7.92	0.91
aaF$_{VFA}$ (mg/h)[3]	887.92 ± 67.08^{a}	479.17 ± 70.42^{b}	764.58 ± 162.92^{ab}	0.035
^{12}C-aaD$_{VFA}$ (mg/h)[4]	1557.92 ± 246.25^{a}	536.67 ± 23.33^{b}	695.83 ± 289.58^{ab}	0.014
^{13}C-aaD$_{VFA}$ (mg/h)[4]	33.75 ± 1.42^{a}	27.50 ± 2.13^{b}	30.83 ± 2.58^{ab}	0.045
aaT$_{VFA}$ (mg/h)[5]	2479.17 ± 250.00^{a}	1080.25 ± 88.75^{b}	1537.92 ± 520.00^{ab}	0.035

Note: Values are presented as means ± SEM, $n=5$ (1 pig/pen).

Abbreviations: SEM, standard error of the mean; VFA, volatile fatty acid.

[a,b]Within rows, values with different superscripts differ ($p \le 0.05$).

[1]LCF is a basal diet of 3% crude fiber; MCF is a basal diet of 4.5% crude fiber; HCF is a basal diet of 6% crude fiber.

[2] ^{12}C-aaC$_p$ is the concentrations of [^{12}C]-acetic acid in the portal vein; ^{12}C-aaC$_a$ is the concentrations of [^{12}C]-acetic acid in the arteria femoralis.

[3] ^{12}C-aaF$_{VFA}$ is the net flux of [^{12}C]-acetic acid in the portal vein; ^{13}C-aaF$_{VFA}$ is the net flux of [^{13}C]-labeled acetic acid in the portal vein; aaF$_{VFA}$ is the net flux of total acetic acid in the portal vein.

[4] ^{12}C-aaD$_{VFA}$ is the deposition of [^{12}C]-acetic acid in the large intestine; ^{13}C-aaD$_{VFA}$ is the deposition of [^{13}C]-labeled acetic acid in the large intestine.

[5]aaT$_{VFA}$ is the net intake of total acetic acid in the large intestine.

TABLE 3 Effect of the different levels of crude fiber supplementation on the net flux of propanoic acid in the portal vein and the deposition of propanoic acid in the large intestine of growing pigs.

Item[1]	LCF	MCF	HCF	*p*-value
$^{12}C\text{-}paC_p$ (mg/L)[2]	100.30 ± 12.95	99.3 ± 12.70	74.40 ± 4.35	0.20
$^{12}C\text{-}paC_a$ (mg/L)[2]	57.85 ± 2.65	59.35 ± 1.95	58.30 ± 1.25	0.87
$^{12}C\text{-}paF_{VFA}$ (mg/h)[3]	232.083 ± 30.83	239.17 ± 60.42	169.58 ± 39.17	0.51
$^{13}C\text{-}paF_{VFA}$ (mg/h)[3]	27.50 ± 11.25	22.92 ± 2.71	30.11 ± 6.66	0.82
paF_{VFA} (mg/h)[3]	253.75 ± 34.58	262.083 ± 59.17	245.10 ± 14.17	0.96
$^{12}C\text{-}paD_{VFA}$ (mg/h)[4]	197.92 ± 35.031[a]	202.50 ± 15.42[a]	83.75 ± 16.67[b]	0.007
$^{13}C\text{-}paD_{VFA}$ (mg/h)[4]	19.58 ± 0.75	17.083 ± 1.29	17.50 ± 0.88	0.25
paT_{VFA} (mg/h)[5]	512.50 ± 19.58[a]	522.50 ± 40.83[a]	353.33 ± 17.50[b]	0.002

Note: Values are presented as means ± SEM, $n = 5$ (1 pig/pen).

Abbreviations: SEM, standard error of the mean; VFA, volatile fatty acid.

[a,b]Within rows, values with different superscripts differ ($p \le 0.05$).

[1]LCF is a basal diet of 3% crude fiber; MCF is a basal diet of 4.5% crude fiber; HCF is a basal diet of 6% crude fiber.

[2] $^{12}C\text{-}paC_p$ is the concentrations of [^{12}C]-propionic acid in the portal vein; $^{12}C\text{-}paC_a$ is the concentrations of [^{12}C]-propionic acid in the arteria femoralis.

[3] $^{12}C\text{-}paF_{VFA}$ is the net flux of [^{12}C]-propionic acid in the portal vein; $^{13}C\text{-}paF_{VFA}$ is the net flux of [^{13}C]-labeled propionic acid in the portal vein; paF_{VFA} is the net flux of total propionic acid in the portal vein.

[4] $^{12}C\text{-}paD_{VFA}$ is the deposition of [^{12}C]-propionic acid in the large intestine; $^{13}C\text{-}paD_{VFA}$ is the deposition of [^{13}C]-labeled propionic acid in the large intestine.

[5] paT_{VFA} is the net intake of total propionic acid in the large intestine.

TABLE 4 Effect of the different levels of crude fiber supplementation on the net flux of butyric acid in the portal vein and the deposition of butyric acid in the large intestine of growing pigs.

Item[1]	LCF	MCF	HCF	*p*-value
$^{12}C\text{-}baC_p$ (mg/L)[2]	68.70 ± 3.70	64.80 ± 2.55	60.10 ± 1.15	0.12
$^{12}C\text{-}baC_a$ (mg/L)[2]	56.25 ± 0.35	55.75 ± 0.55	56.055 ± 3.70	0.37
$^{12}C\text{-}baF_{VFA}$ (mg/h)[3]	73.33 ± 17.50	55.87 ± 10.42	46.25 ± 9.17	0.35
$^{13}C\text{-}baF_{VFA}$ (mg/h)[3]	18.75 ± 5.42	14.58 ± 1.46	20.050 ± 3.88	0.60
baF_{VFA} (mg/h)[3]	92.083 ± 20.42	69.58 ± 10.42	75.00 ± 3.57	0.48
$^{12}C\text{-}baD_{VFA}$ (mg/h)[4]	202.083 ± 28.75[a]	122.92 ± 8.33[ab]	95.32 ± 35.21[b]	0.037
$^{13}C\text{-}baD_{VFA}$ (mg/h)[4]	28.75 ± 0.88	27.50 ± 2.21	28.75 ± 2.38	0.81
baT_{VFA} (mg/h)[5]	302.50 ± 55.12[a]	226.25 ± 8.75[ab]	165.42 ± 18.75[b]	0.044

Note: Values are presented as means ± SEM, $n = 5$ (1 pig/pen).

Abbreviations: SEM, standard error of the mean; VFA, volatile fatty acid.

[a,b]Within rows, values with different superscripts differ ($p \le 0.05$).

[1]LCF is a basal diet of 3% crude fiber; MCF is a basal diet of 4.5% crude fiber; HCF is a basal diet of 6% crude fiber.

[2] $^{12}C\text{-}baC_p$ is the concentrations of [^{12}C]-butyric acid in the portal vein; $^{12}C\text{-}baC_a$ is the concentrations of [^{12}C]-butyric acid in the arteria femoralis.

[3] $^{12}C\text{-}baF_{VFA}$ is the net flux of [^{12}C]-butyric acid in the portal vein; $^{13}C\text{-}baF_{VFA}$ is the net flux of [^{13}C]-labeled butyric acid in the portal vein; baF_{VFA} is the net flux of total butyric acid in the portal vein.

[4] $^{12}C\text{-}baD_{VFA}$ is the deposition of [^{12}C]-butyric acid in the large intestine; $^{13}C\text{-}baD_{VFA}$ is the deposition of [^{13}C]-labeled butyric acid in the large intestine.

[5] baT_{VFA} is the net intake of total propionic acid in the large intestine.

protectors.[6,7] VFAs are the primary products of anaerobic microbial fermentation in the LI.[23,24] Thus, it is vital to quantify the net absorption of VFAs in the LI. In this study, our researchers used an ileum fistula model in pigs, which could separate the LI from the whole GIT. Then, in combination with stable isotope techniques, we quantified the net absorption of VFAs in the LI for pigs with different dietary CF levels.

First, to measure the blood flow rate in the PV, we utilized a well-documented method by constantly injecting P-aminohippuric acid (PAH) into the pigs' ileal mesenteric vein.[19,25] PAH was used as a dilution indicator of blood to measure the blood flow rate. Using five pigs weighing between 33 and 42 kg, a previous study showed that the blood flow rates in the PV during the pre- and postprandial periods were 1163 and 1531 mL/min per pig, respectively.[13] However, in the present study, the blood flow rate in the PV was 56.18–189.87 mL/min per pig. The primary reasons for the differences may be the pigs' body weight, dietary components, and arterial blood sources. Then, the net flux of VFAs in the PV was determined based on the blood collected by cannulation.[20] Another consideration was how to quantitatively determine the net absorption of VFAs in the LI, which should exclude the VFAs left behind in the LI before the experiment

for accurate measurement. In general, the measurements of the abundances of stable isotopes (carbon-13 in the present study) using GC–MS are used as metabolic tracers.[17] The previous study showed that the portal venous blood flow rate tended to be stable after 2 h of feeding.[13] Therefore, it is reasonable to believe that the transport rate of nutrients in the intestine has stabilized after 2 h of feeding. Furthermore, we found no significant differences in the concentrations of [^{12}C]-VFA in the PV for the same pig between the baseline blood sample and the other blood sample based on the results. And the body tissues do not differ in terms of the absorption of VFAs with carbon isotopes.[14] Under these conditions, the ratio of the deposition of [^{12}C]-VFAs in the LI to the deposition of [^{13}C]-VFAs in the LI should be equal to the ratio of the net flux of [^{12}C]-VFA in the PV to the net flux of [^{13}C]-VFA in the PV; thus Equation (A3) can be obtained by conversion. Equations (A2) and (A3) can be employed as a system of equations for determining the deposition of VFAs in the LI. The VFAs absorbed by the LI are transported through the PV and then to the liver for metabolism, so for Equation (A4), the net absorption of VFAs in the LI is equal to the sum of the deposition of VFAs in the LI and the net flux of VFAs in the PV. Note that the Calculation Equations were described in supplementary material.

In the present study, there were no statistically significant differences in the net flux of [^{13}C]-labeled VFAs (acetic acid, propanoic acid, and butyric acid) in the PV or the deposition of [^{13}C]-labeled VFAs (propanoic acid and butyric acid) in the LI, indicating that the PV reflux tissue and the LI had the same ability to absorb VFAs after surgery among the three groups. The transport of VFAs by the large intestinal tissue and the PV was in a dynamic balance during the sampling period. We found that the net flux of acetic acid in the PV and the deposition of [^{12}C]-acetic acid in the LI exhibited the same trends, where there was an initial decrease followed by an increase as the CF level increased. The upward trend might be attributed to the increasing CF levels (LCF vs. MCF) that accelerated the emptying rate of the LI, as suggested in previous studies.[26,27] Then, the downward trend (MCF vs. HCF) might be attributed to providing more fermentable substrates for anaerobic microorganisms in the LI.[28–30] The deposition of [^{12}C]-propionic acid and [^{12}C]-butyric acid in the LI decreased as the CF levels increased. Simultaneously, the LI produces acetic acid at a faster rate than propionic acid and butyric acid.[5] This leads to the rapid emptying rate of the LI with increased CF levels, which may be the main factor affecting the deposition of propionic acid and butyric acid in the LI. Furthermore, the results indicated that the changing trend of the net absorption of total acetic acid did not simply increase as CF levels increased. Previous research studies also documented similar results,[1] which could be attributed to the soluble carbohydrate intake decreases (corn: 56.47% [LCF] vs. 53.00% [MCF]) besides fermentation substrate increases (CF: 4.5% [MCF] vs. 6.0% [HCF]). However, the regulation mechanism of the effects of soluble carbohydrate intake for pigs on the net absorption of total acetic acid in the LI is still unknown and needs further investigation.

Interestingly, we calculated the metabolizable nutrients of this experimental diet (table 1 in supplementary material) based on the theory of systems nutrition.[21] As shown in the Supporting Information Table S2, the sum of the endogenous metabolizable nutrients accounted for about 13.17%–16.10% of the sum of metabolizable nutrients. This supported the studies that VFA production in the LI has been estimated to contribute between 5% and 28% of the maintenance energy requirement of pigs.[5–7] Meanwhile, to verify the creditability and comparability of the results using this method, our researchers evaluated VFA production in the LI in vitro under this experimental diet. Supporting Information, Table S3 shows that unitary linear regression design was used to establish a regression equation of the net absorption of VFAs in the LI in vivo and the production of VFAs in vitro and then checked the goodness of fit.

5 | CONCLUSIONS

In summary, we explored an accurate method for measuring the net absorption of VFAs in the LI by using [^{13}C]-labeled VFA perfusion and blood vessel cannulation; this combined model of a pig quantifies the endogenous nutrients (short chain fatty acid in this study) in the LI, thereby supporting future research on the absorption of nutrients by the LI. We also found the effects of different dietary CF levels on the net absorption of VFAs in the LI in growing pigs. Pigs assigned to LCF had more net absorption of VFAs in the LI compared with MCF and HCF pigs. Nevertheless, additional research is still warranted to properly determine the optimal levels and CF source for pigs in different growth stages.

AUTHOR CONTRIBUTIONS

Data curation: Liangkang Lv. *Funding acquisition*: Shengjun Zhao and Ying Ren. *Methodology*: Shengjun Zhao and Ying Ren. *Project administration*: Liangkang Lv, Zhi Feng, Qiang Li, Long Lei, Zhengya Liu, Taotao Wu, and Hui Zhang. *Writing of the original draft*: Liangkang Lv. *Writing—review and editing*: Liangkang Lv and Ying Ren. All authors contributed equally to the manuscript and read and approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors certify that there is no conflict of interest with any financial organization regarding the content and details assumed in this paper.

ETHICS STATEMENT

The experiment and animal handling procedures were approved by the Animal Care and Use Committee of Wuhan Polytechnic University (2010-0029).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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