

Impact of sugar beet pulp and wheat bran on serum biochemical profile, inflammatory responses and gut microbiota in sows during late gestation and lactation

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Research

Keywords: Dietary fiber source, Gut microbiota, Inflammatory response, Serum biochemical profile, Sow

Posted Date: October 28th, 2020

DOI: <https://doi.org/10.21203/rs.3.rs-96826/v1>

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Version of Record: A version of this preprint was published at Journal of Animal Science and Biotechnology on April 20th, 2021. See the published version at <https://doi.org/10.1186/s40104-021-00573-3>.

Abstract

Background: Sows are frequently subjected to various stresses during late gestation and lactation, which trigger inflammatory response and metabolic disorders. Dietary fiber can influence animal health by modulating gut microbiota and their by-products, with the effects depending upon the source of the dietary fiber. This study aimed to evaluate the impacts of different fiber sources on body condition, serum biochemical parameters, inflammatory responses and fecal microbiota in sows from late gestation to lactation.

Methods: Forty-five multiparous sows (Yorkshire × Landrace; 3-6 parity) were assigned to 1 of 3 dietary treatments from d 85 of gestation to the end of lactation (d 21 post-farrowing): a control diet (CON, a corn-soybean meal diet), a sugar beet pulp diet (SBP, 20% SBP during gestation and 10% SBP during lactation), and a wheat bran diet (WB, 30% WB during gestation and 15% WB during lactation).

Results: Compared with CON, supplementation of SBP decreased ($P < 0.05$) lactation BW loss, reduced ($P < 0.05$) serum concentration of total cholesterol, non-esterified fatty acids, interleukin-6 and tumor necrosis factor- α , and increased ($P < 0.05$) fecal water content on d 110 of gestation and d 21 of lactation, while supplementation of WB reduced ($P < 0.05$) serum concentration of total cholesterol on d 110 of gestation, increased ($P < 0.05$) fecal water content and decreased ($P < 0.05$) serum interleukin-6 concentration on d 110 of gestation and d 21 of lactation. In addition, sows fed SBP had lower ($P < 0.01$) abundance of *Clostridium_sensu_stricto_1* and *Terrisporobacter* than those fed CON, but had greater ($P < 0.05$) abundance of *Christensenellaceae_R-7_group* and *Ruminococcaceae_UCG-002* than those fed the other two diets on d 110 of gestation. On d 21 of lactation, supplementation of SBP decreased ($P < 0.05$) the abundance of Firmicutes and *Lactobacillus*, but enriched ($P < 0.05$) the abundance of *Christensenellaceae_R-7_group*, *Prevotellaceae_NK3B31_group*, *Ruminococcaceae_UCG-002*, *Prevotellaceae_UCG_001* and *unclassified_f_Lachnospiraceae* compared with WB. Compared with CON, sows fed SBP had greater ($P < 0.05$) fecal concentrations of acetate, butyrate and total SCFAs during gestation and lactation, while sows fed WB only had greater ($P < 0.05$) fecal concentration of butyrate during lactation.

Conclusions: Supplementation of dietary fiber during late gestation and lactation could improve sow metabolism and gut health, and SBP was more effective than WB.

Background

Pregnant sows are frequently subjected to psychological and physiological stresses (e.g. rapid fetal development and feed restriction), which can result in oxidative stress and metabolic disorders, and consequently an imbalance inflammatory response [1, 2]. Furthermore, labor-induced injury of the birth canal and uterus can exacerbate oxidative stress and inflammatory responses at parturition [3]. Moreover, even during lactation, the drastic catabolism and anabolism due to milk synthesis also can further contribute to metabolic disorders and inflammatory responses in sows [4, 5]. Long-term exposure to

inflammation may, in turn, induce poor health status or even diseases [6]. Therefore, it is necessary to develop strategies to alleviate inflammatory responses and metabolic disorders in sows, especially during late gestation and lactation.

Recently, gut microbiota has been considered as an important factor of sound health due to its various effects on host [7]. A well-balanced microbiota plays a critical role in maintaining metabolic homeostasis and stimulating immune system development [8]. In contrast, an imbalanced microbiota usually leads to various diseases, in particular obesity, inflammatory bowel disease, diabetes and metabolic syndrome [7, 9]. Generally, whether gut microbiota is beneficial to host health mainly depend on its metabolites derived from fermentation of indigestible substances in diets [10]. As a consequence, manipulation of gut microbiota and its metabolites by dietary modulation may be a potentially effective approach to improve sow health.

Dietary fiber (DF) is a mixture of carbohydrates that are indigestible by host enzymes but subjected to microbial fermentation, generating short chain fatty acids (SCFAs), principally acetate, propionate, and butyrate [11]. These SCFAs derived from DF fermentation, especially butyrate, have been demonstrated to have multiple health benefits, including increase insulin sensitivity, regulate immune system, reduce inflammation, and so on [10]. Previous studies with sows primarily focused on the beneficial effects of DF from a welfare perspective [12, 13]. In addition, some other studies showed that high fiber diets could improve the reproductive performance of sows [14]. However, these studies have overlooked the effects of DF on sow gut health, particularly microbiota. Furthermore, the responses of sows to high fiber diets were inconsistent, possibly due to different physiochemical properties of DF [15]. Sugar beet pulp (SBP) is a pectin-rich soluble fiber source, which is highly fermentable and has been shown to prevent postweaning diarrhea by modulating gut microbiota composition in weaned pigs [16]. Wheat bran (WB) is a source of insoluble fiber, rich in arabinoxylan and cellulose, which also has been shown to alleviate gut inflammation and enhance gut barrier function by improving gut microbiota in mice and weaned pigs [17, 18]. Till now, research with WB and SBP as a source of DF on sow's health status during late gestation and lactation are limited. Therefore, the present study aimed to investigate the effects of supplementing the two sources of DF to sow diets during late gestation and lactation on body condition, serum biochemical parameters, immune responses, fecal microbiota and SCFAs.

Materials And Methods

Animals, diets and management

Animal management and experimental procedures were approved by the Institutional Animal Care and Use Committee of China Agricultural University (Beijing, China). Forty-five healthy multiparous sows (Yorkshire × Landrace; 3-6 parity) were assigned to 1 of 3 dietary treatments balancing for parity, body weight (BW) and backfat thickness from d 85 of gestation to the end of lactation (d 21 post-farrowing). Dietary treatments included a control diet (CON, a corn-soybean meal basal diet), a sugar beet pulp diet (SBP, 20% sugar beet pulp during gestation and 10% sugar beet pulp during lactation), and a wheat bran

diet (WB, 30% wheat bran during gestation and 15% wheat bran during lactation). The experimental two fiber diets had mostly the similar content of total dietary fiber. All diets were formulated to meet or exceed the nutrients requirements for sows as recommended by NRC (2012) (Table 1)[19]. The details nutrient composition of wheat bran (WB) and sugar beet pulp (SBP) are presented in the foot note of Table 1.

Sows were housed in individual gestation stalls (2.1 × 0.6 m) till d 106 of gestation., Then sows were transferred to the farrowing rooms where they were housed in individual farrowing crates (2.1 × 1.5 m) on d 107 of gestation. During gestation, sows were fed twice a day at 0800 and 1600 h, and water was freely available. To achieve the same energy intake per day, sows were fed 3.00 kg/d of CON, 3.09 kg/d of SBP, and 3.31 kg/d of WB, respectively. On the day of farrowing, sows were fed 0.5 kg of lactation diets, and then feed allowance was gradually increased by 1.0 kg/d until ad libitum feeding. All sows also had free access to water during lactation. Within 24 h after farrowing, the litter size was standardized to approximately 11 piglets by cross-fostering within treatment.

Sample collection

Individual body weight and backfat thickness at the last rib were recorded for sows on d 85 and 110 of gestation, within 24 h after farrowing, and at weaning. On d 110 of gestation and d 21 of lactation, blood samples were collected from 6 sows each treatment via the ear vein before feeding. Serum was isolated by centrifugation at 3,000 × *g* and 4°C for 10 min, and frozen at -80°C until analysis. On d 110 of gestation and d 21 of lactation, fresh feces were collected directly by massaging the rectum of sows, and immediately stored at -80°C until analysis.

Fecal water content

Approximately 200 g of fecal samples were oven-dried at 103°C for 72 h. The sample weight before and after oven-dried was recorded to calculate fecal water content.

Serum parameters

Serum samples were thawed at 4°C and mixed thoroughly before analysis. Serum biochemical parameters including urea nitrogen (UN), total cholesterol (TC), triglyceride (TG), non-esterified fatty acids (NEFA) and glucose (GLU) were measured by the commercial kits (Beijing Sino-uk Institute of Biological Technology, Beijing, China) using an automatic biochemical analyzer (Hitachi 7160, Hitachi High-Technologies Corporation, Tokyo, Japan).

Serum concentrations of immunoglobulins including IgA, IgG and IgM and inflammatory cytokines including interleukin-6 (IL-6), interleukin-10 (IL-10) and tumor necrosis factor- α (TNF- α) were measured by enzyme-linked immunosorbent assay kits according to the manufacturer's instructions (Beijing Sino-uk Institute of Biological Technology, Beijing, China).

DNA extraction and 16S RNA sequencing

Bacterial DNA was extracted from fecal samples using a Stool DNA Kit (Omega Bio-tek, Norcross, GA, USA) following the manufacturer's recommendations. The DNA concentration was quantified by NanoDrop 2000 UV-vis spectrophotometer (Thermo Scientific, Wilmington, United States), and the integrity of DNA was checked by 1% agarose gel electrophoresis. The V3-V4 hypervariable region of 16S rRNA gene was amplified with primers F338 (5'-ACTCCTACGGGAGGCAGCAG-3') and R806 (5'-GGACTACHVGGGTWTCTAAT-3'). Then Amplicons were extracted from 2% agarose gels, and purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA) and quantified with a QuantiFluor TM-ST fluorometer (Promega, USA). Purified amplicons were pooled in equimolar concentrations and paired-end sequenced (2 × 300) on an Illumina MiSeq platform according to the standard protocols. Demultiplexing and quality-filtering of raw sequences were performed by QIIME (version 1.17). Then the rest high-quality sequences were clustered into operational taxonomic units (OTU) at 97% similarity by UPARSE and chimeric sequences were identified and removed by UCHIME. Each 16S rRNA gene sequence was taxonomically allocated on the basis of the silva (SSU128) 16S rRNA database by RDP Classifier (<http://rdp.cme.msu.edu/>) with a confidence threshold of 70%.

Fecal short chain fatty acids

Fecal concentrations of SCFAs were analyzed as previously described by Shang et al. (2020) [2]. Briefly, approximately 0.5 g of fecal samples were diluted in 8 mL ultrapure water, homogenized by ultrasonic oscillation, and centrifuged at 12,000 × *g* for 10 min. Then the supernatant was diluted 50 times, filtered through a 0.22-mm filter, and analyzed by a high-performance ion chromatography of ICS-3000 (Dionex, United States). The concentrations of SCFAs were expressed as mg/g of feces.

Statistical analysis

Data were analyzed using SAS 9.2 (SAS Inst. Inc., Cary, NC, USA) with individual sow as an experimental unit. The relative abundance of gut microbial communities was analyzed by Kruskal-Wallis test. Other data were analyzed using GLM procedures followed by Tukey's tests. Significant difference was declared at $P < 0.05$, and tendency was declared at $0.05 \leq P < 0.10$.

Results

Sow body condition

Effects of fiber sources on sow body condition are presented in Table 2. No significant differences were observed in sow BW (d 85 and 110 of gestation, d 1 and 21 of lactation) and backfat thickness (d 85 of gestation, d 1 and 21 of lactation). However, the lactation BW loss was decreased ($P < 0.05$) in sows fed SBP diets when compared with those fed CON diets, but similar with those fed WB diets.

Fecal water content

Effects of fiber sources on fecal water content in sows are presented in Fig. 1. Both SBP and WB supplementation increased ($P < 0.05$) fecal water content in sows on d 110 of gestation (Fig. 1A). The

same response was also observed on d 21 of lactation (Fig. 1B).

Serum biochemical parameters

Effects of fiber sources on serum biochemical parameters in sows are presented in Fig. 2. On d 110 of gestation, a significant decrease ($P < 0.05$) in serum concentration of UN was observed in sows fed SBP when compared with those fed CON. Both sources of fiber supplementation significantly reduced ($P < 0.05$) serum TC concentration. Moreover, sows fed SBP showed a lower ($P < 0.05$) serum concentration of NEFA than those fed the other two diets. No significant differences were detected in serum concentrations of TG and GLU among treatments. On d 21 of lactation, serum concentration of UN was no longer changed by fiber supplementation. However, serum concentrations of TC and NEFA were still decreased ($P < 0.05$) by SBP supplementation when compared with CON. There was still no change in serum concentrations of TG and GLU among treatments.

Serum immunoglobulins

Effects of fiber sources on serum immunoglobulins in sows are presented in Fig. 3. Dietary treatments did not alter serum concentrations of IgA, IgG and IgM on d 110 of gestation or on d 21 of lactation (Fig. 3A and 3B).

Serum inflammatory cytokines

Effects of fiber sources on serum inflammatory cytokines in sows are presented in Fig. 4. On d 110 of gestation, supplementation of both sources of fiber decreased ($P < 0.05$) serum concentration of IL-6 when compared with CON (Fig 4A). Sows fed SBP showed greater ($P < 0.05$) serum concentration of IL-10 than those fed CON, but not different from those fed WB. In addition, the SBP supplementation decreased ($P < 0.05$) serum TNF- α concentration compared with the other two treatments. On d 21 of lactation, the decreased serum IL-6 concentration was also observed in sows fed SBP and WB than those fed CON ($P < 0.05$) (Fig 4B). But dietary treatments did not influence serum IL-10 concentration. Serum TNF- α concentration was lower ($P < 0.05$) in sows fed SBP than those fed CON, but was similar to those fed WB.

Fecal microbiota

To understand the effects of fiber sources on gut microbiota, 16S rRNA gene sequencing of fecal samples were performed. After quality control, a total of 538,051 and 825,315 high-quality sequences were generated from 15 fecal samples on d 110 of gestation and d 21 of lactation, respectively. The average numbers of high-quality sequences generated per sample were 35,870 and 55,021 on d 110 of gestation and d 21 of lactation, respectively. The Venn diagram showed that there were 771, 767, and 710 OTUs obtained from sows fed CON, SBP and WB on d 110 of gestation, of which 630 OTUs were shared and 42 OTUs were unique (Figure 5A). There were 876, 875, and 889 OTUs obtained from sows fed CON, SBP and WB on d 21 of lactation, of which 790 OTUs were shared and 42 OTUs were unique (Figure 5B). The bacterial alpha-diversity (Shannon index) was not significant different among treatments within each period (Figure 6A and 6B). Principal coordinate analysis (PCoA) based on Bray–Curtis dissimilarity

revealed that there was a clear separation of the microbial community among three treatments on d 110 of gestation and d 21 of lactation, indicating a shift in gut microbial communities (Figure 7A and 7B).

Subsequently, the effects of fiber sources on gut microbial composition in sows were investigated. At the phylum level, the dominant phyla during both periods were Firmicutes, Bacteroidetes, and Spirochaetes, accounting for more than 95% (Figure 8A and 8B). On d 110 of gestation, the top three genera in CON were *Clostridium_sensu_stricto_1*, *norank_f__Bacteroidales_S24-7_group*, and *Prevotellaceae_NK3B31_group*; those in SBP were *Treponema_2*, *Christensenellaceae_R-7_group* and *Prevotellaceae_NK3B31_group*; and those in WB were *norank_f__Bacteroidales_S24-7_group*, *Lactobacillus* and *Clostridium_sensu_stricto_1* (Figure 8C). On d 21 of lactation, the top three genera in CON were *Treponema_2*, *norank_f__Bacteroidales_S24-7_group* and *Lactobacillus*; those in SBP were *Treponema_2*, *Lachnospiraceae_XPB1014_group*, and *Christensenellaceae_R-7_group*; and those in WB were *Lactobacillus*, *norank_f__Bacteroidales_S24-7_group* and *Clostridium_sensu_stricto_1* (Figure 8D).

Differential analysis of microbial composition among treatments were further explored. At the phylum level, sows fed SBP had greater ($P < 0.05$) abundance of phyla Treponema than those fed WB on d 110 of gestation (Figure 9A), while supplementation of WB enriched ($P < 0.05$) the abundance of Firmicutes compared with SBP on d 21 of lactation (Figure 9B). At the genus level, on d 110 of gestation, the SBP supplementation significantly decreased ($P < 0.01$) the abundance of *Clostridium_sensu_stricto_1* and *Terrisporobacter* compared with CON (Figure 10A). Sows fed SBP had greater ($P < 0.05$) abundance of *Christensenellaceae_R-7_group* and *Ruminococcaceae_UCG-002* than those fed the other two diets. In addition, supplementation of WB reduced ($P < 0.01$) the abundance of *Ruminococcaceae_UCG-002* when compared with CON. On d 21 of lactation, sows fed WB and CON had greater ($P < 0.05$) abundance of *Lactobacillus* than those fed SBP (Figure 10B). Compared with WB, the SBP supplementation enriched ($P < 0.05$) the abundance of *Christensenellaceae_R-7_group*, *Prevotellaceae_NK3B31_group*, *Ruminococcaceae_UCG-002*, and *Prevotellaceae_UCG_001*. In addition, sows fed SBP had greater ($P < 0.05$) abundance of *unclassified_f__Lachnospiraceae* than those fed the other two diets.

Fecal short chain fatty acids

Effects of fiber sources on fecal short chain fatty acids in sows are presented in Fig. 11. On d 110 of gestation, fecal concentrations of acetate, butyrate and total SCFAs were increased ($P < 0.05$) in sows fed SBP diets compared with those fed CON diets, but not different from those fed WB diets (Figure 11A). There were no differences observed in fecal concentrations of propionate, isobutyrate, valerate and isovalerate among treatments. On d 21 of lactation, compared with sows fed CON diets, sows fed SBP diets had greater ($P < 0.05$) fecal concentrations of acetate, butyrate and total SCFAs, while sows fed WB diets had greater ($P < 0.05$) fecal concentration of butyrate (Figure 11B). There were also no differences in fecal concentrations of propionate, isobutyrate, valerate and isovalerate among treatments.

Discussion

During lactation, sows mobilize their body reserves to support milk synthesis, which generally leads to body loss at weaning [20]. Sow body condition at weaning is known to be closely associated with its reproductive performance as a good body condition plays a vital role in maintaining a good reproductive performance, while in contrast, a poor body condition has adverse impacts on the subsequent reproduction performance by prolonging weaning-estrous interval and decreasing litter sizes [21]. In the present study, sows fed SBP showed lower lactation weight loss than those fed CON, suggesting a better body condition. Similarly, Renteria-Flores et. al [22] also observed a lower lactation weight loss in sows fed high fiber diet compared with those fed the control diet. However, the results were not always consistent as some researches failed to detect positive effects of high fiber diets on lactation weight loss in sows [23]. The discrepancies for the consistent results may be due to the sources, inclusion levels of fiber as well as feeding duration and stage of animals [13, 24].

It is well known that constipation is a common symptom for pregnant sows because gastrointestinal motility was decreased, and transit time was significantly prolonged during pregnancy, thereby resulting in increased water absorption and eventually low frequency and hard stools [25]. Constipation can lead to a series of distressing symptoms, including abdominal distension, gut obstruction, perforation, and increased farrowing duration, thereby affecting health of sows [26]. In this study, greater fecal water content was observed in sows fed SBP and WB diets when compared with those fed CON diets, suggesting that high fiber diets may alleviate the constipation severity in pregnant sows by retaining fecal water content. Our results were in consistent with previous studies, in which high fiber diets containing konjac flour or alfalfa meal increased fecal water content and relieved constipation in pregnant sows [27, 28]. Dietary fiber generally has great water-binding capacity, and also can reduce transit time and increase stools bulk, which may contribute to the alleviative constipation [29, 30].

Serum biochemical parameters are useful biomarkers for monitoring body health and physiological condition [31]. Protein that escapes digestion in the foregut is fermented partly in the hindgut into ammonia, which is either used as nitrogen source for microbiota or absorbed into blood and transformed to urea in the liver [32, 33]. Therefore, blood urea nitrogen can reflect nitrogen utilization efficiency in various animal species [34]. In this study, sows fed SBP diets showed lower serum urea nitrogen concentration compared with those fed CON diets during gestation, indicating greater nitrogen utilization efficiency in sows fed SBP. Similarly, previous studies also revealed that fermentable fiber could reduce plasma urea nitrogen in growing pigs and sows [24, 35]. One possible explanation is that as substrates for bacteria, fermentable fiber can increase bacterial mass, which, in turn, utilizes more ammonia as nitrogen for protein synthesis, thereby reducing urea nitrogen absorption into blood [35]. Another possible explanation is that dietary fiber can suppress protein fermentation, thereby reducing ammonia production [36]. However, a part of our results indicated that sows fed WB diets did not show lower serum urea nitrogen concentration compared with CON, which may be because soluble fiber has a greater capacity to increase microbial mass and activity in comparison with insoluble fiber [37].

An interesting finding in this study is that sows fed both SBP and WB had lower serum TC concentration compared with those fed CON during gestation. Our results were in consistent with Ndou et al. [38], in

which both soluble fiber (flaxseed meal) and insoluble fiber (oat hulls) decreased serum total cholesterol concentration in pigs, showing hypocholesterolemic effects. As a source of soluble fiber, the SBP can increase digesta viscosity, and hence increase cholesterol and bile acid excretion, which may in turn influence hepatic cholesterol metabolism, and eventually result in decreased serum cholesterol concentration [39]. While as a source of insoluble fiber, the WB can increase cholesterol and bile acid excretion by shortening transit time of digesta in the gastrointestinal tract [38].

It is well known that NEFA are a product of fat metabolism and a good indicator of catabolism of fat reserves [40]. In the current study, the decreased serum NEFA concentration observed in sows fed SBP might suggest reduced fat metabolism, and therefore better body reserve. Indeed, this study demonstrated that sows fed SBP had a lower body loss during lactation though no significant difference was observed in backfat loss among treatments. In contrast, the WB supplementation did not influence serum NEFA concentration when compared with CON. It has been shown that the SCFAs production was negatively correlation with serum NEFA concentration and fermentable fiber could decrease serum NEFA concentration by increasing SCFAs production [41]. The SBP contains more soluble fibers (e.g. pectin) that are readily fermentable than WB, therefore, more SCFAs were produced in sows fed SBP as evidenced by increased fecal concentration of total SCFAs.

Pregnancy is generally associated with a systemic inflammatory response, which has adverse effects on both maternal and fetal health [1]. In the current study, lower serum concentration of pro-inflammatory cytokine IL-6 was observed in sows fed SBP and WB during pregnancy and lactation, suggesting alleviative inflammatory responses by fiber supplementation. In addition, sows fed SBP also showed lower serum concentration of pro-inflammatory cytokine TNF- α and greater serum concentration of anti-inflammatory cytokine IL-10 than those fed CON, indicating that SBP may be more effective in reducing inflammation than WB. It is known that IL-10, an anti-inflammatory cytokine, can suppress proinflammatory responses by decreasing cytokine and chemokine production [42]. Thereby, the SBP may relieve inflammation by increasing the production of anti-inflammatory cytokine IL-10. Likewise, previous studies also found that higher intake of dietary fiber was closely related to decreased severity of inflammation, in contrast, dietary fiber deprivation resulted in inflammation and increased pathogen susceptibility [43–45]. The positive effects of dietary fiber on inflammation observed in this study may be correlated to the changed gut microbiota and their by-products induced by the two sources of fiber supplementation [46].

Intestinal microbiota plays a crucial role in maintaining host health by regulating metabolism and immune system [47, 48]. In the present study, even if there were no significant changes in α -diversity among three treatments within each period, principal coordinates analysis (PCoA) showed a distinct clustering for each dietary treatment at both periods, illustrating that different fiber sources induce significant differences in gut microbial composition. Generally, Firmicutes and Bacteroidetes were the most dominant phyla in most mammals [49]. In this study, Firmicutes and Bacteroidetes were indeed the most abundant phyla in all treatments regardless of the period, which was consistent with fecal microbiota from sows reported in previous studies [50, 51]. However, sows fed SBP showed an increased

abundance in phyla Tenericutes during gestation when compared with those fed WB. Previous studies demonstrated that a decrease in the abundance of Tenericutes was associated with intestinal inflammation [52, 53]. Therefore, the high abundance of Tenericutes in SBP-fed sows may have resulted from the low level of the inflammatory response. Interestingly, the WB supplementation increased the abundance of Firmicutes compared with SBP during lactation. It has been shown that an increased abundance in Firmicutes is generally associated with a greater capacity of energy absorption from the diet and a greater feed conversion ratio [54, 55]. The increased abundance of Firmicutes during lactation would be thus desired because lactating sows need more energy to maintain the requirements of themselves and their offspring.

Certain changes were also observed at the genus level in sows fed different fiber sources. During gestation, the SBP supplementation significantly decreased the abundance of *Clostridium_sensu_stricto_1* compared with CON. *Clostridium_sensu_stricto_1* is usually considered as pathogenic bacteria as well as an indicator of a less healthy microbiota [56, 57]. It has been reported that the enrichment of *Clostridium_sensu_stricto_1* was associated with the high transcript levels of pro-inflammatory cytokines in the sheep colon, impaired intestinal barrier function in pigs and necrotizing enterocolitis in preterm infants [58–60]. As a result, the decrease in the abundance of *Clostridium_sensu_stricto_1* may be an indicator of a healthy microbiota and a contributor to the reduced concentrations of inflammatory cytokines. Furthermore, sows fed SBP had greater abundance of *Christensenellaceae_R-7_group* and *Ruminococcaceae_UCG-002* than those fed the other two diets. *Christensenellaceae* is recently identified as health-promoting bacteria due to its positive effects on body mass index, immunomodulation and healthy homeostasis [61, 62]. *Ruminococcaceae* is known to produce short-chain fatty acids by degrading various polysaccharides and fibers [63]. *Ruminococcaceae_UCG-002*, a genera belonging to the family *Ruminococcaceae*, can ferment indigestible carbohydrates into butyrate, which plays an essential role in maintaining intestinal health and function [64, 65]. As a consequence, the increase abundance of *Christensenellaceae_R-7_group* and *Ruminococcaceae_UCG-002* would be favourable for intestinal health in sows fed SBP.

During lactation, the increased abundance of *Christensenellaceae_R-7_group* and *Ruminococcaceae_UCG-002* were observed in sows fed SBP as well. In addition, the SBP supplementation also enriched the abundance of *Prevotellaceae_NK3B31_group*, *Prevotellaceae_UCG_001* and *unclassified_f_Lachnospiraceae*. *Prevotellaceae* and *Lachnospiraceae* are known to be beneficial bacteria which are associated with polysaccharide fermentation and SCFAs generation [66, 67]. It has been reported that healthy pigs had a higher abundance of *Prevotellaceae* and *Lachnospiraceae* compared with diarrhoeic pigs [68]. Wang et al. [69] also reported that the increased abundance of *Prevotellaceae_NK3B31_group* contributed to alleviate the diarrhea of weaned pigs challenged with enterotoxigenic *Escherichia coli* K88. In a mice model of ulcerative colitis, *Prevotellaceae_UCG_001* has been shown to positively associated with anti-inflammatory cytokines (e.g. IL-4 and IL-10) and inversely correlate with pro-inflammatory cytokines (e.g. IL-1, IL-6, IL-8, and TNF- α), exerting an anti-inflammatory effect [70]. Therefore, these results, taken together, demonstrated that supplementation of SBP induced a more healthy microbiota in sows.

An interesting finding in this study was that sows fed WB had greater abundance of *Lactobacillus* than those fed SBP during lactation. Moreover, during gestation, sows fed SBP also showed high abundance of *Lactobacillus* although no significant difference was observed among treatments. *Lactobacillus* species are well-known probiotics on account of their multiple health-promoting effects, including suppression of intestinal inflammation, enhancement of intestinal barrier function, modulation of immune responses, maintenance of microbial homeostasis and prevention of diseases [71–73]. Therefore, the WB supplementation may improve sow health by the increased abundance of *Lactobacillus*.

There is growing evidence that microbial metabolite short-chain fatty acids are key executors of diet-based microbial effect on the host [10]. Changes in intestinal microbial composition are generally accompanied by changes in the production of SCFAs [74]. In this study, fecal concentrations of acetate, butyrate and SCFAs were increased by SBP supplementation compared with CON during gestation. The same patterns were also observed during lactation, suggesting greater microbial fermentation in the gut. *Prevotellaceae_NK3B31_group* has been shown to be positively correlated with acetic acid production [66]. *Ruminococcaceae* and *Lachnospiraceae* are well-known butyrate-producing bacteria [75]. *Ruminococcaceae_UCG-002* was reported to produce butyrate by fermenting indigestible carbohydrates, while *Christensenellaceae* can produce acetate and butyrate [62, 76]. Consequently, the increased concentrations of acetate and butyrate could be attributed to the increased abundance of *Ruminococcaceae_UCG-002*, *Christensenellaceae_R-7_group*, *Prevotellaceae_NK3B31_group* and *unclassified_f_Lachnospiraceae* by SBP supplementation. An important finding in this study was that both fiber sources could increase fecal concentration of butyrate. Butyrate is the most effective SCFA, which not only provides energy for colonocytes, but also maintain gut homeostasis by inhibiting inflammation and carcinogenesis, reinforcing barrier function and alleviating oxidative stress [77]. As a result, the increased concentration of butyrate may contribute to be lower inflammatory response and better health in sows.

Conclusions

In conclusion, both SBP and WB supplementation could improve metabolism, immune responses and gut health in sows but by differently affecting microbiota. In addition, the SBP was more effective than WB in terms of these indexes.

Abbreviations

BW, body weight; CON, control diet; DF, dietary fiber; GLU, glucose; IgA, immunoglobulins A; IgG, immunoglobulins G; IgM, immunoglobulins M; IL-6, interleukin-6; IL-10, interleukin-10; NEFA, non-esterified fatty acids; OUT, operational taxonomic units; PCoA, principal coordinate analysis; SBP, sugar beet pulp diet; SCFAs, short chain fatty acids; TC, total cholesterol; TG, triglyceride; TNF- α , tumor necrosis factor- α ; UN, urea nitrogen; WB, wheat bran diet.

Declarations

Acknowledgements

Not applicable.

Author's contributions

The experiment was designed by Qinghui Shang, and conducted by Qinghui Shang, Sujie Liu and Hansuo Liu. Experimental data were collected and analyzed by Qinghui Shang. The manuscript was written by Qinghui Shang, and revised by Shad Mahfuz and Xiangshu Piao. All authors have read and approved the final manuscript.

Funding

This research was financially supported by National Natural Science Foundation of China (31772612) and the Beijing Municipal Natural Science Foundation (6202019).

Availability of data and material

All data generated or analyzed during this study are included in this published article.

Ethics approval and consent to participate

Animal management and experimental procedures were approved by the Institutional Animal Care and Use Committee of China Agricultural University (Beijing, China).

Consent for publication

Not applicable.

Competing interests

There are no conflicts to declare.

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Tables

Table 1
Ingredients and nutrient composition of experimental diets (% , as-fed basis).

Item	Gestation			Lactation		
	CON	SBP	WB	CON	SBP	WB
Corn	73.65	54.55	50.80	69.74	59.05	54.98
Soybean meal	22.00	21.50	15.00	26.00	26.00	23.00
Wheat bran ¹	-	-	30.00	-	-	15.00
Sugar beet pulp ²	-	20.00	-	-	10.00	-
Soybean oil	0.85	0.85	0.85	0.65	1.53	3.50
Dicalcium phosphate	1.28	1.35	0.57	1.45	1.50	1.10
Limestone	1.07	0.60	1.48	0.78	0.54	0.97
Salt	0.40	0.40	0.40	0.40	0.40	0.40
L-Lysine HCl	-	-	0.15	-	-	0.06
Valine	-	-	-	0.23	0.23	0.24
Premix ³	0.50	0.50	0.50	0.50	0.50	0.50
Chromium oxide	0.25	0.25	0.25	0.25	0.25	0.25
Calculated composition						
Digestible energy, Kal/kg	3353	3259	3037	3388	3388	3388
Available phosphorus	0.31	0.31	0.31	0.34	0.34	0.34
SID lysine	0.69	0.69	0.70	0.78	0.79	0.78
SID methionine	0.22	0.19	0.20	0.23	0.22	0.22
SID threonine	0.49	0.46	0.45	0.53	0.52	0.51
SID tryptophan	0.14	0.14	0.13	0.16	0.16	0.16
SID valine	1.05	1.04	1.02	0.85	0.85	0.85
Analyzed composition						
Crude protein	15.29	15.41	15.48	17.21	17.25	17.21
Calcium	0.74	0.76	0.75	0.68	0.70	0.68
Total phosphorus	0.56	0.55	0.58	0.60	0.59	0.62
Total dietary fiber	11.37	21.60	21.81	11.82	16.83	16.88

Item	Gestation			Lactation		
	CON	SBP	WB	CON	SBP	WB
Soluble dietary fiber	1.39	4.06	1.86	1.43	2.72	1.69
Insoluble dietary fiber	9.98	17.54	19.95	10.39	14.11	15.18
¹ Nutrient composition of wheat bran: dry matter, 89.37%; organic matter, 83.55%; crude protein, 17.12%; gross energy, 17.01 MJ/kg; neutral detergent fiber, 37.36%; acid detergent fiber, 11.55%; total dietary fiber, 44.57%; soluble dietary fiber, 3.89%; insoluble dietary fiber, 40.68%.						
² Nutrient composition of sugar beet pulp: dry matter, 91.42%; organic matter, 84.63%; crude protein, 10.29%; gross energy, 15.62 MJ/kg; neutral detergent fiber, 38.25%; acid detergent fiber, 23.48%; total dietary fiber, 61.69%; soluble dietary fiber, 17.12%; insoluble dietary fiber, 44.57%.						
³ Premix provided per kilogram of diet: Gestation: vitamin A, 11,000 IU; vitamin D ₃ , 1,500 IU; vitamin E, 15 IU; vitamin K ₃ , 1.6 mg; vitamin B ₁ , 1.5 mg; vitamin B ₂ , 3.0 mg; vitamin B ₆ , 1.5 mg; vitamin B ₁₂ , 0.015 mg; niacin, 22.5 mg; D-pantothenic acid, 15 mg; folic acid, 2.5 mg; biotin, 0.2 mg; Fe, 85 mg; Cu, 7.5 mg; Zn, 75 mg; Mn, 35 mg; I, 0.5 mg; Se, 0.3 mg; Lactation: vitamin A, 6,500 IU; vitamin D ₃ , 1,550 IU; vitamin E, 15.5 IU; vitamin K ₃ , 1.6 mg; vitamin B ₁ , 1.6 mg; vitamin B ₂ , 3.1 mg; vitamin B ₆ , 1.5 mg; vitamin B ₁₂ , 0.015 mg; niacin, 23 mg; D-pantothenic acid, 15.5 mg; folic acid, 2.5 mg; biotin, 0.2 mg; Fe, 85 mg; Cu, 10 mg; Zn, 100 mg; Mn, 50 mg; I, 0.5 mg; Se, 0.3 mg.						
CON, control diet; SBP, sugar beet pulp diet; WB, wheat bran diet; SID, standardized ileal digestible.						

Table 2
Effects of fiber sources on sow body condition.

Item	CON	SBP	WB	SEM	<i>P</i> -value
Sow BW, kg					
d 85 gestation	232.5	235.7	228.7	4.35	0.53
d 110 gestation	253.6	258.0	251.7	4.03	0.52
Gestation gain	21.1	22.4	23.0	1.89	0.78
d 1 of lactation	228.2	233.6	228.1	4.15	0.56
Weaning	216.0	223.6	216.9	4.17	0.38
Lactation loss	12.2 ^a	10.0 ^b	11.1 ^{ab}	0.56	0.03
Backfat thickness, mm					
d 85 of gestation	13.53	13.80	13.47	0.60	0.92
d 1 of lactation	14.67	15.00	14.53	0.65	0.87
Gestation gain	1.13	1.20	1.07	0.24	0.92
Weaning	12.07	12.93	12.27	0.68	0.65
Lactation loss	2.60	2.07	2.27	0.23	0.27
^{a-b} Mean values within a row with different letters differ at $P < 0.05$.					
CON, control diet; SBP, sugar beet pulp diet; WB, wheat bran diet.					

Figures

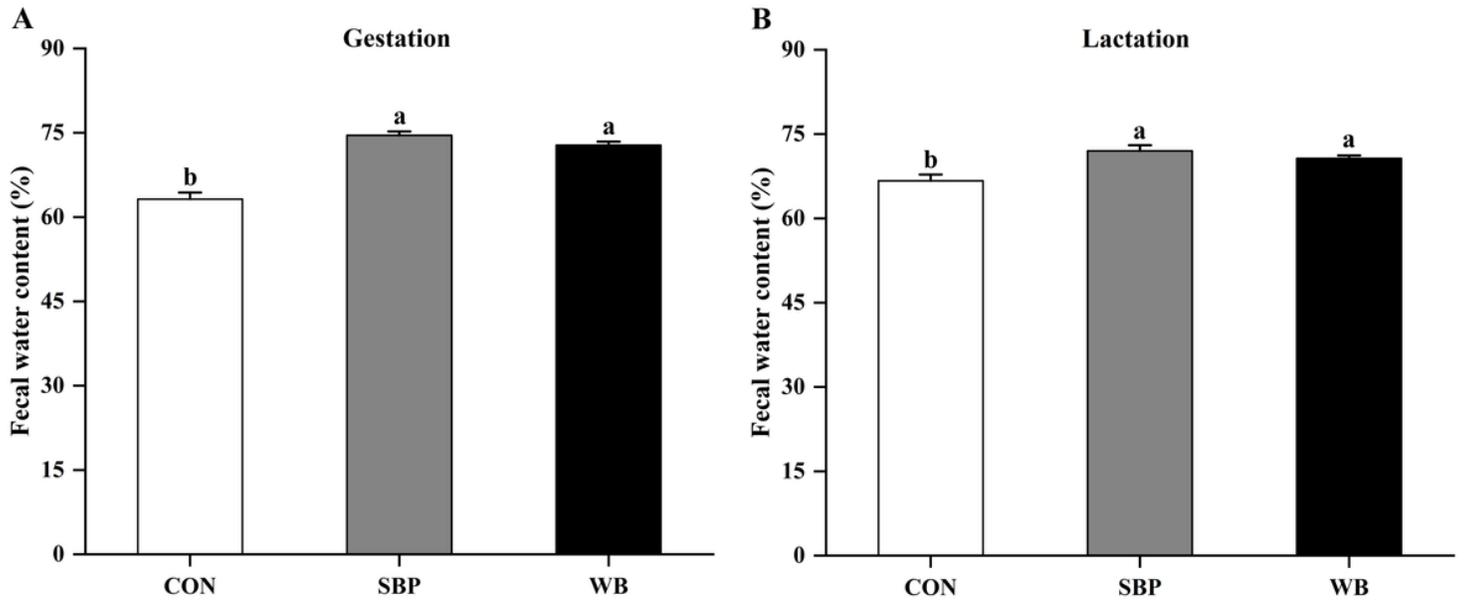


Figure 1

Effects of fiber sources on fecal water content in sows. (A-B) Fecal water content on d 110 of gestation and d 21 of lactation. Data were presented as mean \pm SEM, n = 6. Different letters mean significant differences ($P < 0.05$).

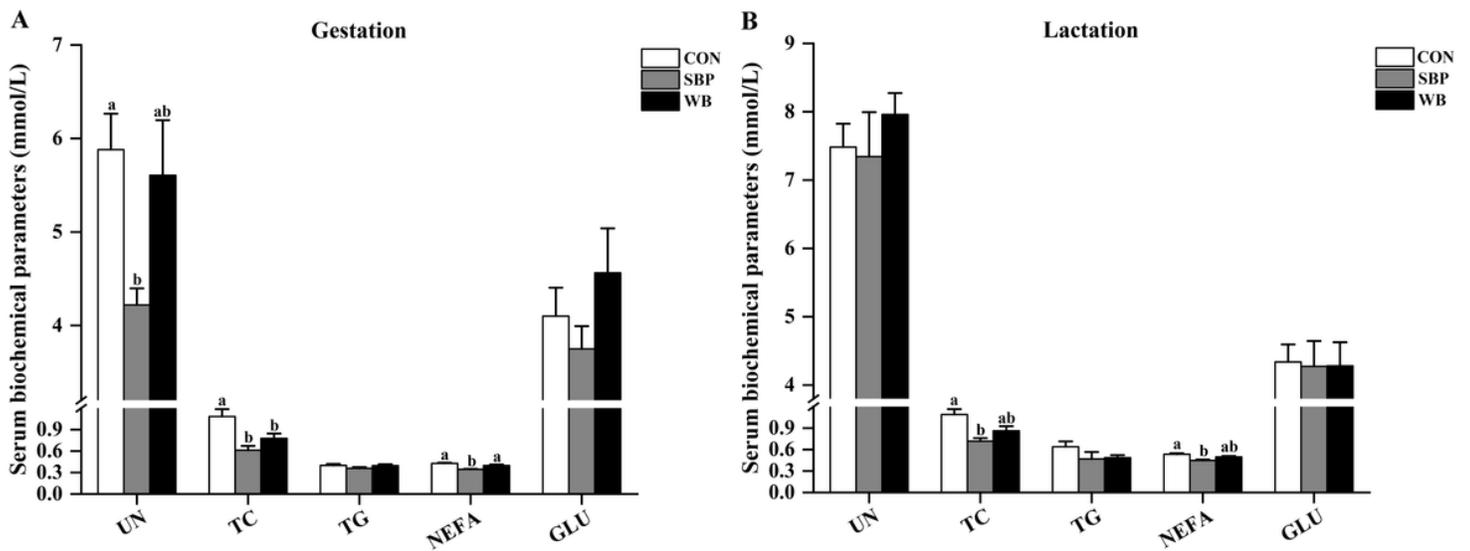


Figure 2

Effects of fiber sources on serum biochemical parameters in sows. (A-B) Serum biochemical parameters on d 110 of gestation and d 21 of lactation. Data were presented as mean \pm SEM, n = 6. Different letters mean significant differences ($P < 0.05$). UN, urea nitrogen; TC, total cholesterol; TG, total triglycerides; NEFA, non-esterified fatty acids; GLU, glucose; CON, control diet; SBP, sugar beet pulp diet; WB, wheat bran diet.

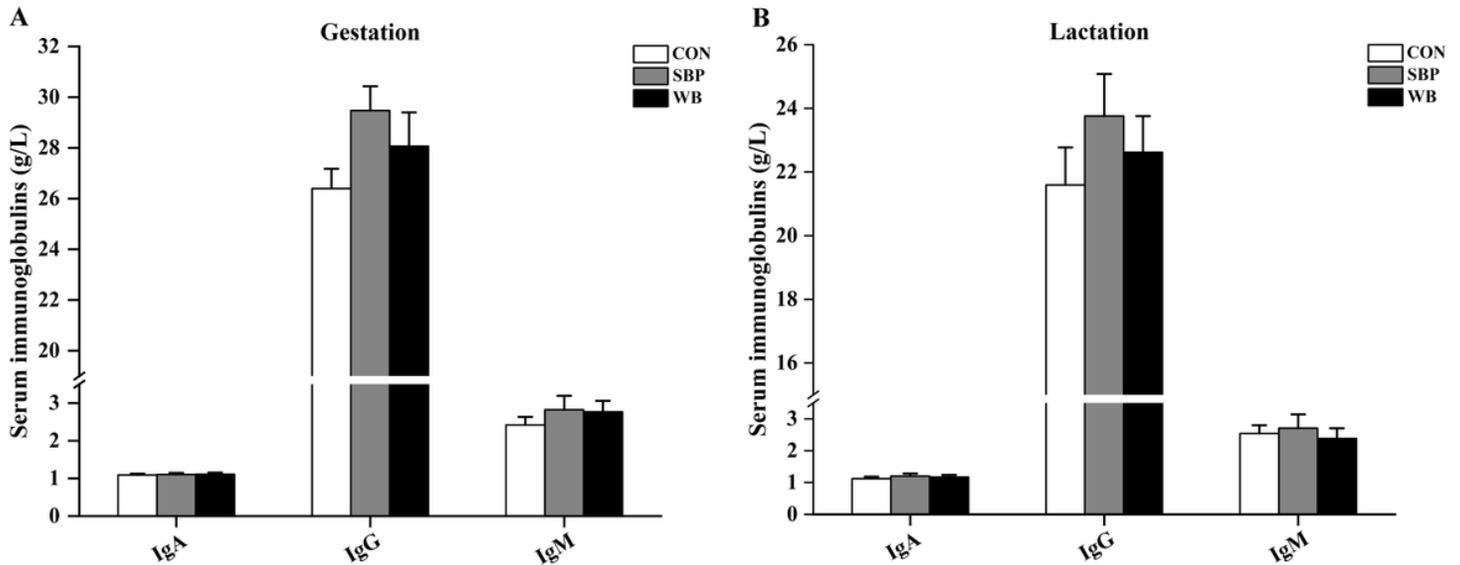


Figure 3

Effects of fiber sources on serum immunoglobulins in sows. (A-B) Serum immunoglobulins on d 110 of gestation and d 21 of lactation. Data were presented as mean \pm SEM, n = 6. Different letters mean significant differences ($P < 0.05$). IgA, immunoglobulin A; IgG, immunoglobulin G; IgM, immunoglobulin M; CON, control diet; SBP, sugar beet pulp diet; WB, wheat bran diet.

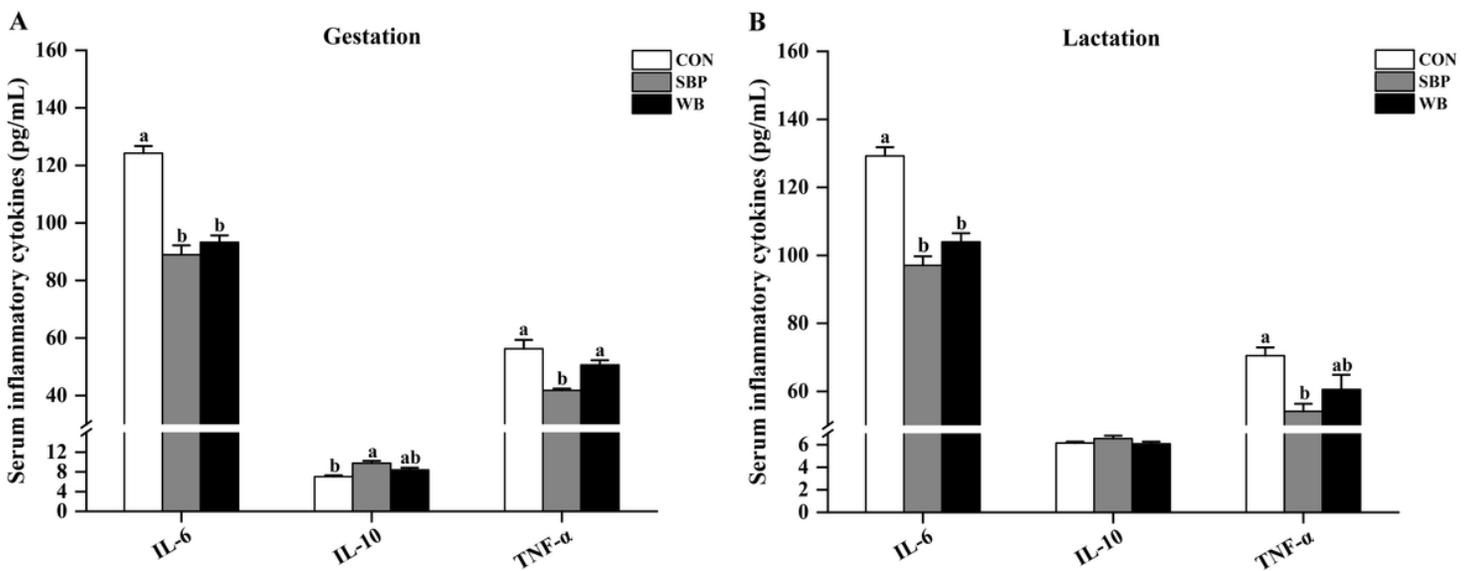


Figure 4

Effects of fiber sources on serum inflammatory cytokines in sows. (A-B) Serum inflammatory cytokines on d 110 of gestation and d 21 of lactation. Data were presented as mean \pm SEM, n = 6. Different letters mean significant differences ($P < 0.05$). IL-6, interleukin-6; IL-10, interleukin-10; TNF- α , tumor necrosis factor- α ; CON, control diet; SBP, sugar beet pulp diet; WB, wheat bran diet.

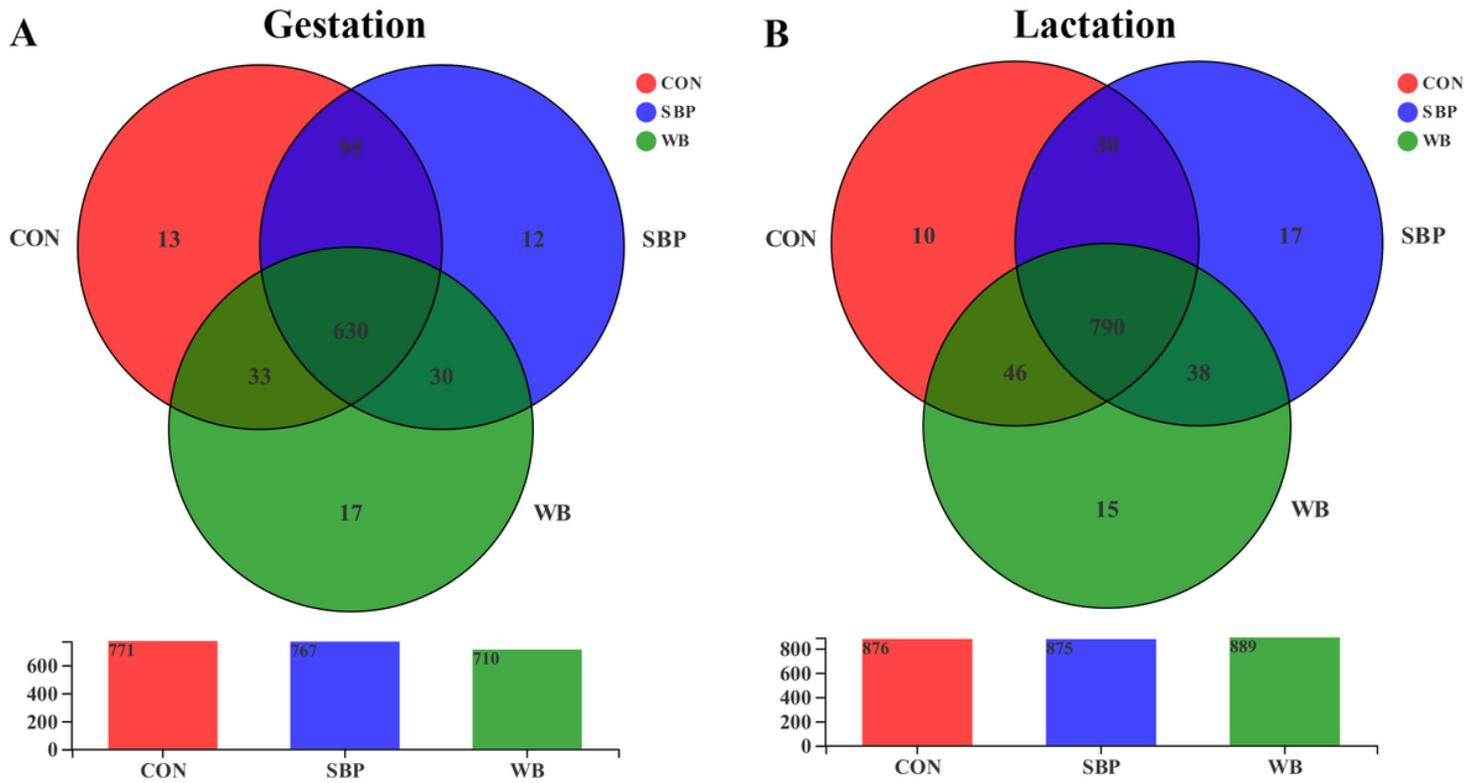


Figure 5

Venn diagram of the operational taxonomic units (OTUs) in sow feces on d 110 of gestation (A) and d 21 of lactation (B). n = 5. CON, control diet; SBP, sugar beet pulp diet; WB, wheat bran diet.

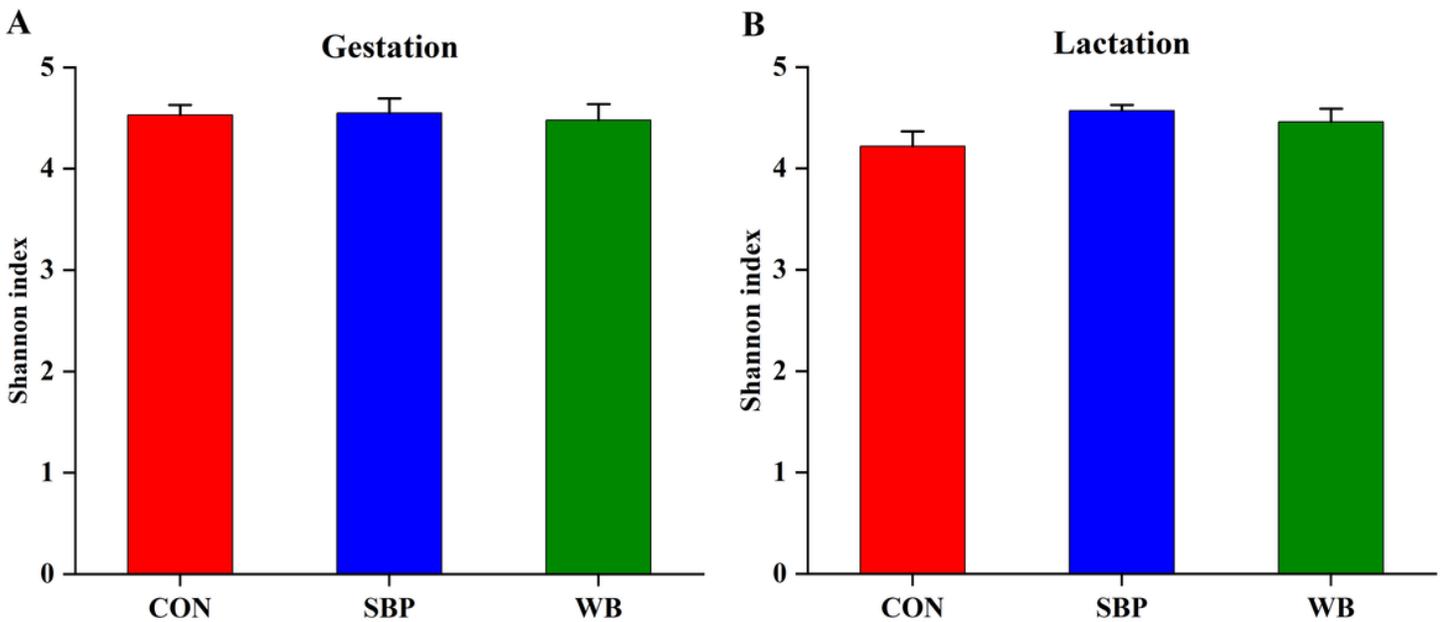


Figure 6

Alpha diversity of fecal microbial community determined by Shannon index on d 110 of gestation (A) and d 21 of lactation (B). n = 5. CON, control diet; SBP, sugar beet pulp diet; WB, wheat bran diet.

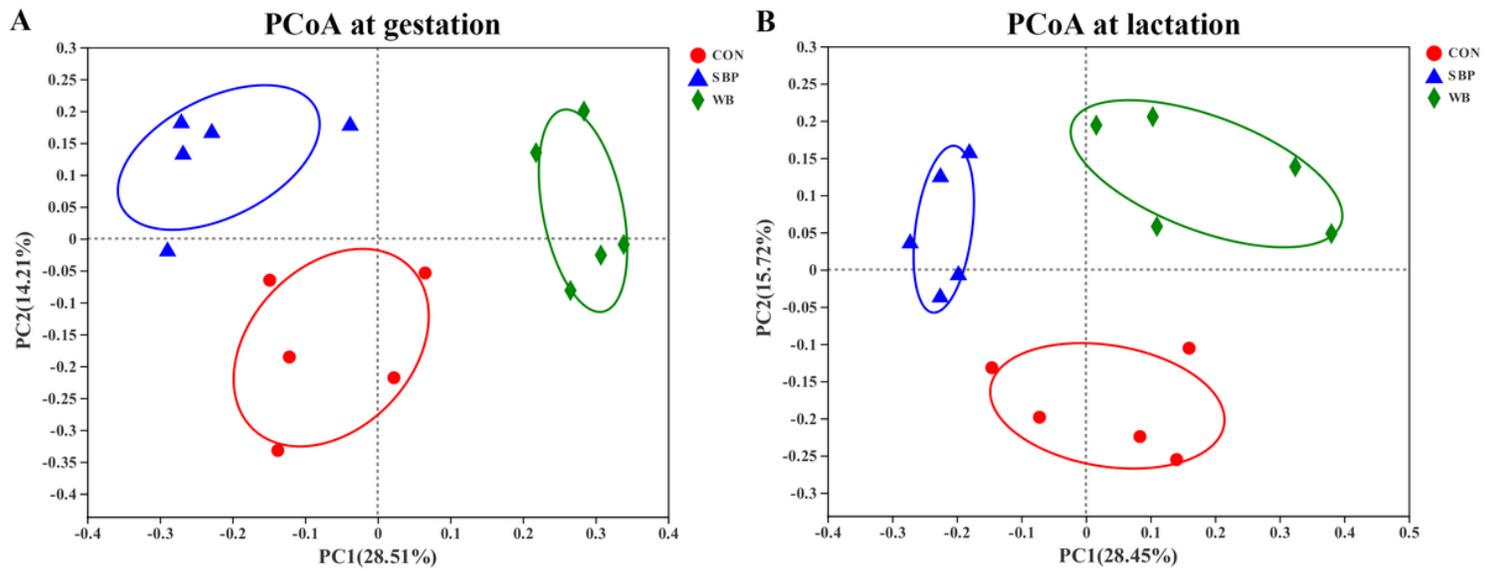


Figure 7

Principal coordinate analysis (PCoA) at the operational taxonomic unit (OTU) level based on Bray–Curtis dissimilarity on d 110 of gestation (A) and d 21 of lactation (B). n = 5. CON, control diet; SBP, sugar beet pulp diet; WB, wheat bran diet.

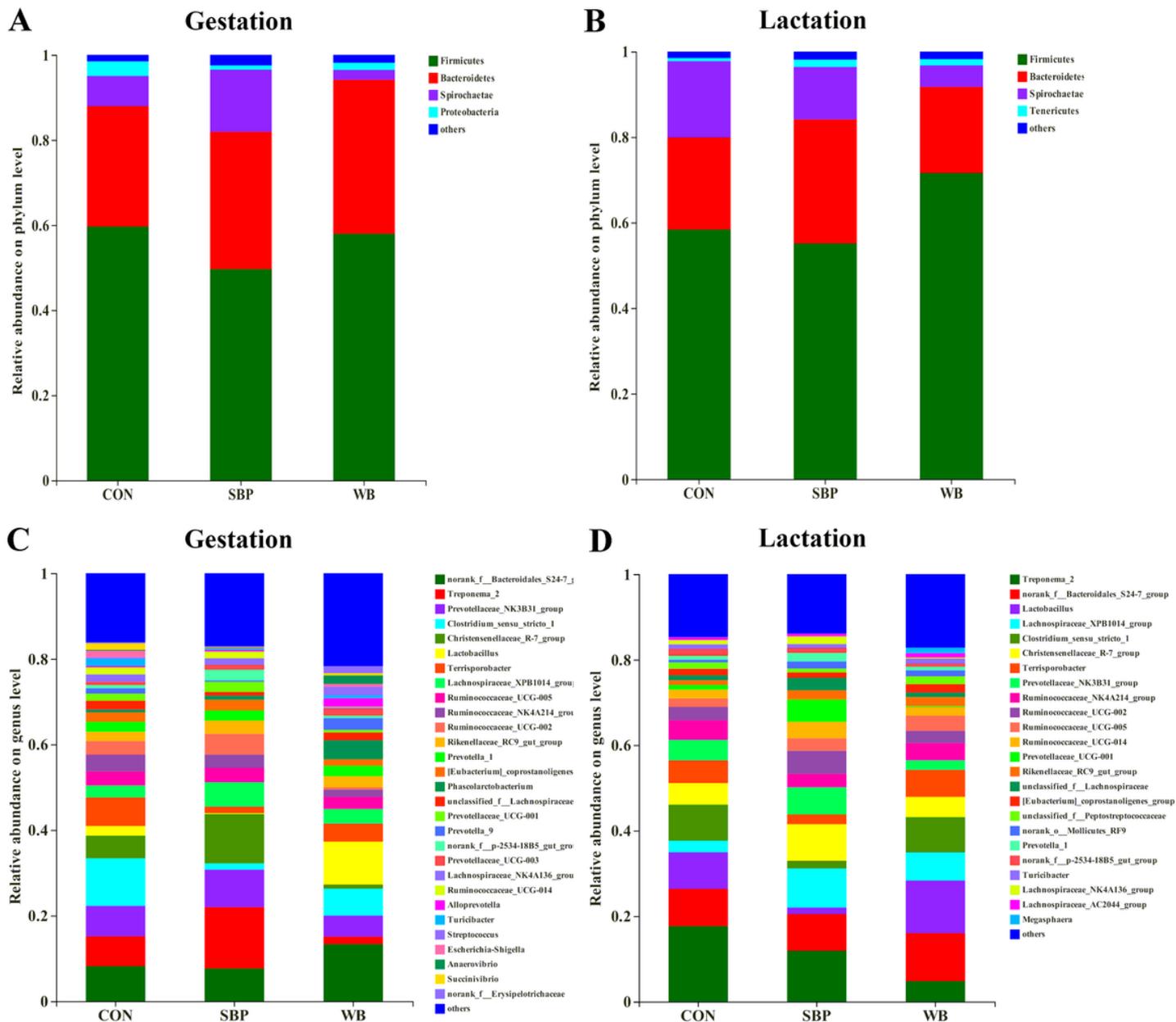


Figure 8

Effects of fiber sources on fecal microbiota composition in sows. (A-B) Microbial community bar plot at the phylum level on d 110 of gestation and d 21 of lactation. (C-D) Microbial community bar plot at the genus level on d 110 of gestation and d 21 of lactation. n = 5. CON, control diet; SBP, sugar beet pulp diet; WB, wheat bran diet.

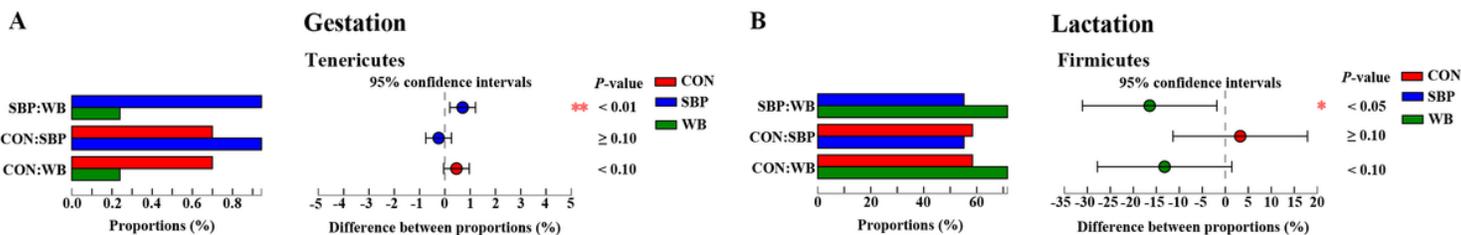


Figure 9

Relative abundance of significantly different phyla on d 110 of gestation (A) and d 21 of lactation (B). n = 5. CON, control diet; SBP, sugar beet pulp diet; WB, wheat bran diet.

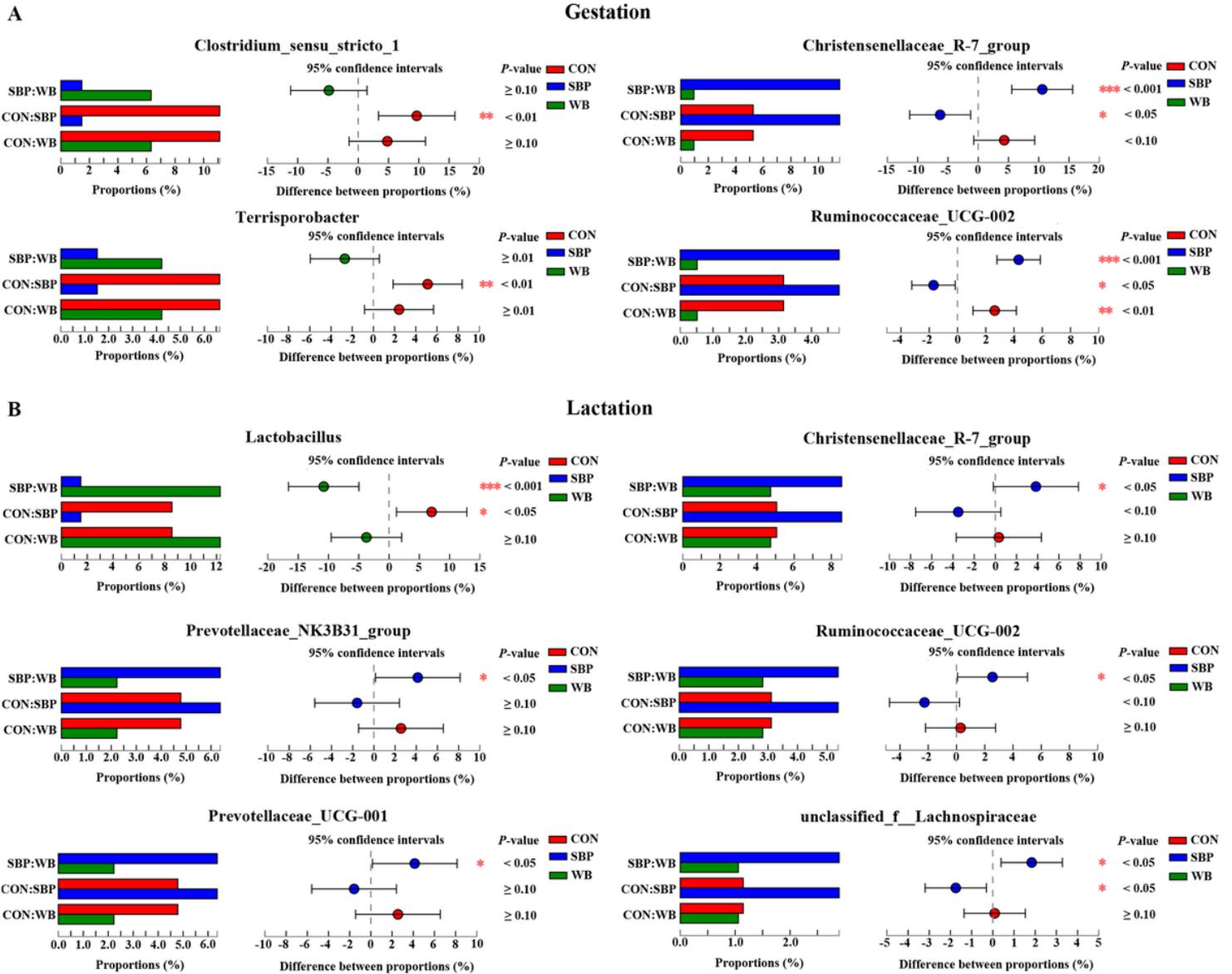


Figure 10

Relative abundance of significantly different genera on d 110 of gestation (A) and d 21 of lactation (B). n = 5. CON, control diet; SBP, sugar beet pulp diet; WB, wheat bran diet.

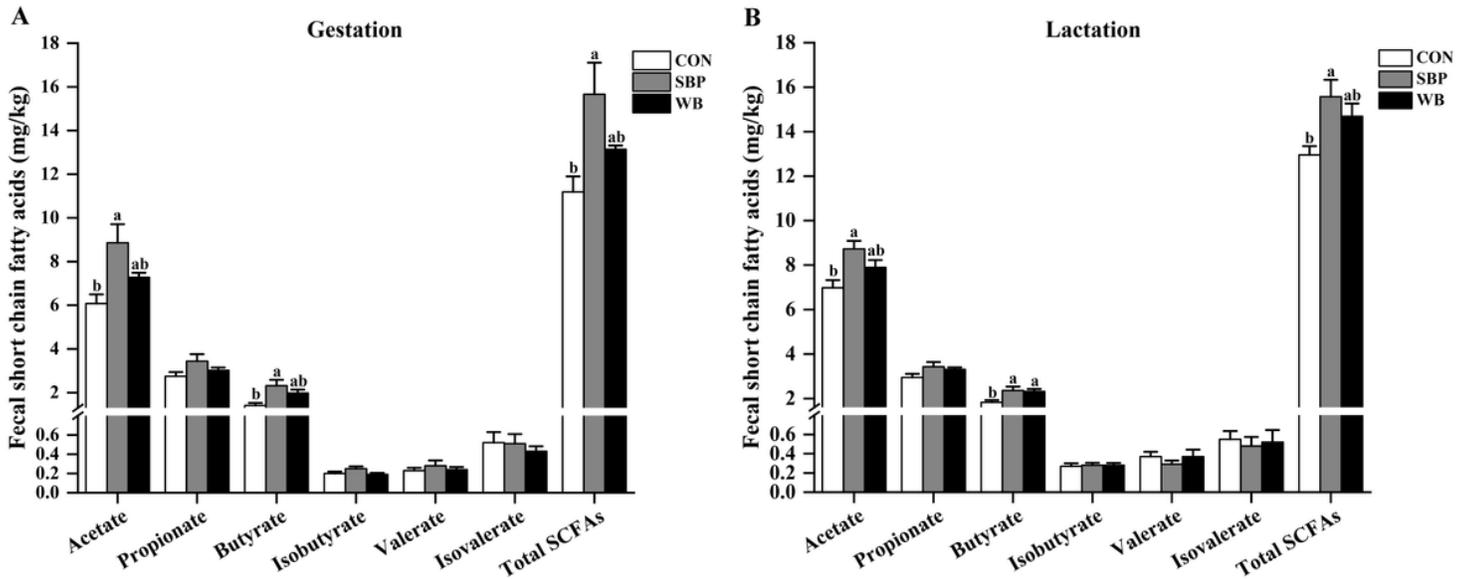


Figure 11

Effects of fiber sources on fecal short chain fatty acids in sows. (A-B) Fecal short chain fatty acids on d 110 of gestation and d 21 of lactation. Data were presented as mean \pm SEM, n = 5. Different letters mean significant differences ($P < 0.05$). SCFAs, short chain fatty acids; CON, control diet; SBP, sugar beet pulp diet; WB, wheat bran diet.