Review Article

Dietary fiber and microbiota interaction regulates sow metabolism and reproductive performance

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A B S T R A C T  

Dietary fiber is a critical nutrient in sow diet and has attracted interest of animal nutritionists for many years. In addition to increase sows’ satiety, dietary fiber has been found to involve in the regulation of multiple biological functions in the sow production. The interaction of dietary fiber and gut microbes can produce bioactive metabolites, which are of great significance to sows’ metabolism and reproductive performance. This article reviewed the interaction between dietary fiber and gut microbes in regulating sows’ gut microbial diversity, intestinal immune system, lactation, and production performance, with the aim to provide a new strategy for the use of dietary fiber in sow diets.

1. Introduction

During gestation, sows are restrictively fed to maintain normal reproductive performance. However, excessive feeding restrictions makes it difficult for sows to produce satiety and sows show abnormal behaviors such as vacuum chewing, frequent rising and lying during pregnancy, which leads to a negative impact on their reproductive performance (Sekiguchi and Koketsu, 2004). In addition, the feed intake of sows during pregnancy is closely related to their voluntary feed intake during lactation. Excessive feeding restriction during pregnancy will result in a decrease in sows’ voluntary feed intake during lactation (Matte et al., 1994; Sun et al., 2014, 2015). Dietary fiber supplementation is an efficient way to maintain proper satiety for sows. Dietary fiber is not easily digested by digestive enzymes in the gastrointestinal tract, thus avoiding the sow from taking in excessive energy (Huang et al., 2020).

Interestingly, dietary fiber not only increases the satiety, but also improves reproductive performance and lactation performance of sows. Previous studies have found that adding dietary fiber to diets during pregnancy increased the total litter birth, weaning litter weights, and milk fat content in colostrum (Che et al., 2011; Loisel et al., 2013; Matte et al., 1994; Veum et al., 2009). Moreover, sows fed with dietary fiber during multiple reproductive cycles have better reproductive and lactation performances (Che et al., 2011; Matte et al., 1994; Veum et al., 2009). The physiological metabolism of sows undergoes complex changes during pregnancy. As a result, the stability of the intestinal flora structure is fragile and easily broken (Newbern and Freeman, 2011). The destruction of intestinal flora stability results in intestinal epithelium damage and intestinal inflammation. The gut microbiota is sensitive to the physical and chemical properties of specific dietary fibers. Many recent studies have reported that the addition of dietary fibers to diets during pregnancy effectively alters sow gut microbiota composition and diversity, and their interaction affects the sow’s
nutritional, physiological, and immune processes in a variety of ways (Cheng et al., 2018a; Jarrett and Ashworth, 2018; Wu et al., 2020; Xu et al., 2020a; Zhuo et al., 2020). The present review summarized the effects of dietary fiber on the composition and diversity of sows’ gut microbes, as well as their interactions on the regulation of sows’ gut health, and reproductive and lactation performances.

2. Changes of gut microbiota composition during different stages of pregnancy

During the reproductive cycle, the physiology and metabolism of the sow undergo complex changes. Gut microbes play a vital role in the function and health of their host (such as, nutrient absorption, metabolism, immune system, and resistance to pathogens) and are also affected by changes in the physiological state of their host. Therefore, the relationship between pregnancy and gut microbes is of particular concern. With the increase of gestational age, the alpha diversity of gut microbiota is also increased. Kong et al. (2016) and Ji et al. (2017) analyzed the ileal and colonic luminal microbiota composition of Huajiangni mini-pigs during pregnancy. From the first to third trimester of pregnancy, the dominant bacteria in the colon of Huajiangni mini-pigs are Firmicutes and Bacteroides, and the dominant genera include Lactobacillus, Prevotella, Ruminococcus, Clostridium, and Prevotella (Kong et al., 2016). And, Firmicutes (account for 69.99% to 85.44% of the total reads) and Proteobacteria (5.82% to 15.17%) are dominant in the ileum (Ji et al., 2017). From the 45th day to the 75th day of pregnancy, the number of Firmicutes and Lactobacillus bacteria in the ileum is decreased, which is contrast to the number of Proteobacteria, Enterobacteriaceae, and Bacteroides. The significant increase of Proteobacteria (mainly pathogenic bacteria) is an indicator of ileal inflammation (Flint et al., 2008; Koren et al., 2012; Wu et al., 2011).

These changes of intestinal microbes could further regulate the metabolism of the host. Recently, Huang et al. (2019) analyzed the gut microbe characteristics of sows from late pregnancy (5 d before delivery) to postpartum (within 6 h after delivery). The results showed that the ratio of Bacteroidetes to Firmicutes and the relative abundance of Prevotella were significantly reduced, and the dominant genus Lactobacillus was significantly increased. Consistent with these changes, the predicted functional capacities of the gut microbe associated with glycan biosynthesis, amino acid metabolism, and the metabolism of cofactors and vitamins were significantly decreased. However, the abundance of the functional capacities related to carbohydrate and lipid metabolism were increased. Intriguingly, it has also been reported that the progression of pregnancy is related to several carbohydrate-degrading bacteria (Prevotella, Succinivibrio, Bacteroides, and Parabacteroides) (Ji et al., 2019). In addition, from pregnancy to parturition, changes in the composition of gut microbes also modified the intestinal levels of pro-inflammatory IL-6 and anti-inflammatory IL-10 (Cheng et al., 2018b). Thus, the interaction of gut microbes at different stages of pregnancy affects the metabolism of the host, which may increase nutrient metabolism and regulate sows’ lactation performance.

3. Dietary fiber regulates the abundance and diversity of sow gut microbes

Dietary fiber has an intimate relationship with the intestinal microbes (Makki et al., 2018). Generally, fiber is divided into soluble fiber and insoluble fiber. The amount of soluble and insoluble fiber varies in different feed ingredients (Jarrett and Ashworth, 2018). Soluble fiber (such as inulin) is hardly digested in the mouth, stomach, and small intestine. This fiber is transported to the hindgut as intact molecules and broken down by the coliform, which produce a small amount of energy and various bioactive substances (Makki et al., 2018). Insoluble fiber (such as cellulose) is difficult to be fermented by intestinal microbes, which could enhance intestinal health by promoting intestinal peristalsis (Capuano, 2017). Firmicutes and Actinobacteria are dominant responders in the gut to break down dietary fiber (Deehan et al., 2017). The digestibility for fiber could be different in the different breeds of sows. For example, Rongchang sows are more capable of digesting high-fiber feed compared with Landrace sows, which is related to the abundant Ruminococcaceae in the gut of Rongchang sows (Liu et al., 2019).

Difference in dietary fiber sources and gut microbiota sensitivity partly determine the complex microbial system of the gut. In sows, Bacteroides and Firmicutes are the most dominant phyla in the intestine, accounting for about 73% of the total sequence of microorganisms (Niu et al., 2019). Moreover, Lactobacillus, Oscillibacter, and Treponema accounted for more than 49% of the total sequence (Niu et al., 2019). There is a close relationship between the gut microbiota composition and the apparent digestibility of crude fiber. For example, the abundance of some microorganisms in sow fecal samples was positively correlated with the apparent digestibility of crude fiber (such as Anaerovibrio and Ruminostomum), neutral detergent fiber (such as Collinsella and Sutterella), and acid detergent fiber (such as Clostridium, Collinsella, Robinsoniella, and Turicibacter). Dietary fiber is the main source of energy for gut microbiota, which means that adding an appropriate amount of dietary fiber can increase the abundance of specific microorganisms (Sappok et al., 2015). In addition, dietary fiber also increases the proportion of beneficial bacteria and reduces the proportion of pathogenic bacteria in the gut (Guan et al., 2019; Jiang et al., 2019; Wu et al., 2020; Xu et al., 2020a).

Therefore, dietary fiber can improve the utilization of protein and fat by regulating the abundance of specific gut microbes. The strategy for dietary fiber to regulate protein fermentation in the intestine has been summarized before (Jha and Berrocoso, 2016). Briefly, dietary fiber effectively relieves the adverse effects of certain amino acid fermentation products (for example, ammonia, histamine) and decreases the harmful strains (such as, enterotoxigenic strains of Escherichia coli) on the intestinal tract. Furthermore, dietary fiber reduced the sow weight gain and fat accumulation that are caused by adding fat in diets (Zhou et al., 2017), which might be caused by the modification of gut microbial structure. These results indicate that dietary fiber can regulate the utilization of protein and fat by intestinal microorganisms, which further promotes sows’ intestinal health.

In summary, the addition of different levels and types of dietary fiber are related to the gut microbiota abundance and diversity. However, for the level of dietary fiber added to the diet, there is currently insufficient data to form a reference standard. Moreover, the research on the effect of dietary fiber types on the gut microbes of sows is still in the preliminary exploratory stage and a large amount of data is still needed to enrich this aspect.

4. Biological effects of dietary fiber fermentation by-products in the gut

Dietary fiber is a critical energy source for cecal and colonic epithelial cells (Fig. 1). Under specific intestinal environmental conditions, dietary fiber is fermented and utilized by anaerobic bacteria and produces a variety of metabolites, such as short-chain fatty acids (SCFA), especially acetate, propionate and butyrate (Jarrett and Ashworth, 2018; Patil et al., 2020). They are an important substrate of gluconeogenesis and participate in the regulation of central metabolism. Short-chain fatty acids trigger
host signals by inhibiting histone deacetylase (HDAC) or activating G protein-coupled receptors (such as GPR41 and GPR43), which are activated to regulate the release of glucagon-like peptide 1 (GLP-1) and neuropeptide Y which lead to satiety.

Short-chain fatty acids involved in the regulation of sow metabolism, immunity, and cell proliferation (Li et al., 2019; Wu et al., 2020; Xu et al., 2020a). Dietary supplementation of 3% purified fiber-mixture significantly increase the concentrations of butyrate and propionate in the feces of sows, which was related to the increase in the abundance of Eubacterium-hallii-group and Bacteroides in the gut (Wu et al., 2020). Different types of dietary fiber contribute to the variation of SCFA (Tokach et al., 2019). Short-chain fatty acids are transported to the peripheral circulation through the portal vein, thereby acting on the liver and peripheral tissues. They have been proposed to act as signal molecules to regulate different physiological activities of the host (Koh et al., 2016), such as regulating immunity and the expression of antioxidant enzymes, inflammatory and pro-inflammatory factors (Li et al., 2019; Shang et al., 2019; Guo et al., 2020; Xu et al., 2020a).

5. Embryo development and survival

To date, it has been widely accepted that dietary fiber supplementation improves the survival rate of sow embryos during pregnancy. Oocytes are very sensitive to maternal nutrient levels. Dietary nutrients intake changes the physiological levels of circulating hormones and metabolites, which ultimately affects the function of the ovaries (Ashworth et al., 2009). Administration of fiber promotes the maturation of follicles and oocytes in the sow ovary (Ferguson et al., 2007; Renteria-Flores et al., 2008; Weaver et al., 2013). The proportions of oocytes reaching Metaphase II were higher in the diet fiber group than in the control group (Weaver et al., 2013).

The modification of ovary function may be due to the dietary fiber fermentation products in the gut. Short-chain fatty acids could bind with G protein-coupled receptors GPR41 and GPR43 and activate their downstream target proteins in the gut. Adenosine 5’-monophosphate-activated protein kinase (AMPK)/mammalian target of rapamycin complex 1 (mTORC1) is a classic signaling pathway which largely regulates cellular biology and metabolism. This pathway also has an important significance for the activation and survival of primordial follicles (Zhuo et al., 2019). Short-chain fatty acids mediates multiple beneficial effects on the host metabolism through the activation of AMPK (Hu et al., 2010). AMPK is a negative regulator of mTORC1. Consistently, the phosphorylation level of mTORC1 and its downstream target S6 in the ovary decrease linearly with the increase of dietary fiber (Cao et al., 2019). In addition, the extracellular signal-regulated protein kinases 1/2 (ERK1/2) signal is also suppressed as the level of dietary fiber increases (Cao et al., 2019). Inhibition of ERK1/2 decrease the mTORC1 signaling, which participates in the activation of primordial follicles. These results indicate that increasing the level of dietary fiber intake can preserve a greater reserve of primordial follicles. Interestingly, these results show that the mTOR signaling pathway is inhibited. Whether this result is really beneficial to the reserve of primordial follicles still needs more evidence.

The other potential pathway for dietary fiber to regulate follicular maturation is through neuropeptide Y. This may be the result of the fermentation of dietary fiber by microorganisms in the intestine. However, to date, there is no direct evidence that microorganisms play a key role in this process. Neuropeptide Y has been shown to be involved not only in regulating food intake, but also related to the secretion of gonadotropin releasing hormone. A high-fiber diet changes the circulating concentrations of estradiol and luteinizing hormone, which are important for oocyte maturation (Ferguson et al., 2007). These results also explain why long-term feeding of dietary fiber increases the total number of births of sows, whereas short-term feeding does not. Because sows fed dietary fiber for a long time not only retain a larger reserve of primordial follicles, but also create a better physiological environment for follicle maturation than short-term feeding sows and gilts.

6. Milk composition

Milk is a unique nutrition source for newborns. During pregnancy and lactation, the mammary gland is one of the most active tissues in sows. In order to provide enough nutrients for newborns, a large amount of nutrients absorbed by the gut are transported to the mammary glands through the blood circulation to synthesize milk. Dietary nutrient level is an important factor affecting the synthesis and composition of sow milk. Although dietary fiber cannot be used directly by sows, its fermentation product is an important source of nutrients for sow milk synthesis. As we mentioned before, dietary fiber could be fermented by gut microorganisms to produce SCFA (Fig. 2). Mammary glands use SCFA as precursors for de novo synthesis of milk fat. Compared with the low-fiber group, the high-fiber group had increased milk fat content in the colostrum (Loisel et al., 2013; Feyera et al., 2019).

The effects of dietary fiber on milk immunoglobulin (Ig) secretion is inconsistent. Loisel et al. (2013) and Feyera et al. (2019) found the concentrations of IgA and IgG in colostrum of sows in the high-fiber group was reduced. Whereas, Shang et al. (2019) reported the concentration of IgA in sow colostrum is significantly increased.
when sows were fed the high-fiber diet. These inconsistent results may be due to the different types of dietary fibers (Loisel et al., 2013; Shang et al., 2019). Recent studies also reported that dietary fiber increases the IL-10 concentration of sow colostrum and normal milk, which is critical to promote piglet intestinal health (Lv et al., 2018; Shang et al., 2019). There is no doubt that the utilization of dietary fiber by sows requires intestinal microbial fermentation, which leads to the changes of related physiological indicators. Unfortunately, these studies did not explore the role of gut microbes in this process.

In addition to nutrients, milk also contains a lot of microorganisms. It is proposed that a portion of the milk microorganisms may derive from the gut, but there is yet a definite conclusion (Moossavi and Azad, 2019; Rodriguez, 2014; Zhang et al., 2018). During the third trimester of pregnancy and lactation, there is an important outflow of intestinal immune cells to the mammary glands (Macpherson and Uhr, 2004; Newburg, 2005; Rescigno et al., 2001; Vazquez-Torres et al., 1999). Gut microbes might transfer into the lymph nodes with the help of dendritic cells (DC) and then reach the mammary gland through the intestinal-lymphatic circulation system. In rats, transplanting Lactobacillus or faecal microbes from healthy rats into polycystic ovary syndrome rats increases the abundance of Lactobacillus in the gut and significantly increases the plasma concentrations of estradiol and estrone (Guo et al., 2016). In sows, the plasma reproductive hormone levels (oestradiol, follicle-stimulating hormone, and luteinizing hormone) in sows with a short WEI (not more than 7 d) are significantly higher than those with a long WEI (>14 d) sows (Xu et al., 2020b). Importantly, in the gut of sows with short WEI, Prevotella and Bacteroides are lower at the genus level, whereas Firmicutes and Lentisphaerae are higher at the phylum level (Xu et al., 2020b). Prevotella and Bacteroides are important genera that degrade carbohydrates in the gut, which indicates dietary fibers might regulate WEI of sows. To our surprise, most studies have shown that increasing dietary fiber has no significant

7. Weaning-to-estrus interval

The weaning-to-estrus interval (WEI) is a crucial indicator to evaluate the reproductive performance of sows. During the reproductive cycle, a relatively fixed WEI (approximately 5 to 7 d) is essential for sows to ovulate efficiently and maintain the embryo survival rate during pregnancy. Estrus is a complex physiological activity and regulated by a variety of reproductive hormones, such as follicle stimulating hormone, luteinizing hormone, and estradiol. The bidirectional interaction between gut microbes and the secretion and metabolism of host sex hormones has been demonstrated (Markle et al., 2013; Melvin, 2016). In rats, transplanting Lactobacillus or faecal microbes from healthy rats into polycystic ovary syndrome rats increases the abundance of Lactobacillus in the gut and significantly increases the plasma concentrations of estradiol and estrone (Guo et al., 2016). In sows, the plasma reproductive hormone levels (oestradiol, follicle-stimulating hormone and luteinizing hormone) in sows with a short WEI (not more than 7 d) are significantly higher than those with a long WEI (>14 d) sows (Xu et al., 2020b). Importantly, in the gut of sows with short WEI, Prevotella and Bacteroides are lower at the genus level, whereas Firmicutes and Lentisphaerae are higher at the phylum level (Xu et al., 2020b). Prevotella and Bacteroides are important genera that degrade carbohydrates in the gut, which indicates dietary fibers might regulate WEI of sows. To our surprise, most studies have shown that increasing dietary fiber has no significant
effect on the WEL of sows. Thus, the minor effects of microorganisms on the secretion of reproductive hormones might not efficiently modify the WEL of sows.

8. Effects on offspring piglets

The beneficial effects of the interaction between dietary fiber and gut microbes can be passed from the mother to the offspring. Dietary fiber is reported to enhance the reproduction performance of sows. Wu et al. (2020) fed gestational sows with a diet supplemented with 3% purified fiber-mixture, which significantly increased the number of live-born piglets. Veum et al. (2009) reported feeding sows a diet supplemented with wheat straw for a long period significantly increased the number of weaned piglets per litter, the weight of total litter births, and weaning weight. Furthermore, a short-term addition of dietary fiber in the late pregnancy also reduced the proportion of stillborn piglets and the total mortality of piglets during lactation (Feyera et al., 2017). The effects of dietary fiber on reproduction performance of sows might be partially dependent on the physical condition of sows and dietary fiber level. Che et al. (2011) fed sows with 3 fiber levels (10.8%, 15.8% and 20.8% neutral detergent fiber) for 2 reproductive cycles. In the first parity, the total litter births, litter births alive, and litter weight in the low-fiber group were significantly higher than those in other groups; likewise, the low-fiber group and medium-fiber group had greater litter weights at parturition and weaning. However, in the second parity, the total number of births, the total litter births and litter births alive, and litter weight in the medium-fiber group were significantly higher than those in other groups. Interestingly, the high-fiber group had the highest survival rate and heavier weight of piglets at weaning (after 22 d of lactation) compared with other groups. These results indicate that sows fed dietary fiber-added diets for a long time is more conducive to improving its production performance, and the addition level of fiber in the diet can be appropriately increased with the extension of feeding time. Some recent studies reported that the changes of sow production performance caused by dietary fiber is related to the modification of gut microbes. Intestinal microbes may lead to the changes of intestinal antioxidant capacity (Zhou et al., 2017). Adding inulin to high-fat diets enhanced the activities of superoxide dismutase (T-SOD) and glutathione peroxidase (GSH-Px) and reduced the malondialdehyde (MDA) concentrations in the serum of sows (Wang et al., 2016). The production performance and antioxidant capacity of sows are positively correlated with Bacteroides of Bacteroidaceae, but negatively correlated with Phascolarctobacterium and Streptococcus (Wang et al., 2019a,b; Wang et al., 2018). It worth noting that T-SOD, GSH-Px, and MDA could be transferred from sows to piglets through milk (Chen et al., 2019a; Chen et al., 2019b; Chen et al., 2020; Wang et al., 2019a,b). Thus, there is a close relationship between dietary fiber, gut microbes, antioxidant abilities, and sow production performance.

9. Conclusion

The application value of dietary fiber in improving the satiety of sows has long been recognized. However, some recent reports suggested that dietary fiber has many other benefits in production of sow. With the reduction in the use of antibacterial drugs on a global scale, the application value of dietary fiber is particularly valued. Dietary supplementation of fiber can change the abundance and diversity of gut microbiota and thereby promote gut health and reduce the need for antibiotics. In addition, the application of dietary fiber to sow diets provides opportunities to improve sow production and reproduction in several aspects. Dietary fiber and gut microbiome interaction affects the diversity and abundance of gut microbes, immune system, milk composition, embryonic development, and the production performance of sows. However, there are still many problems that need to be resolved: 1) The source of dietary fiber is rich and the composition is complex, which makes it difficult to determine a reference standard in production; 2) People’s understanding of gut microbes mostly stays at the level of phylum and genus, which makes it difficult to isolate the key bacteria related to dietary fiber fermentation; 3) A large number of obligate anaerobic bacteria are present in the milk and passed to the piglets. Do these bacteria come from the gut of the sow? Therefore, although dietary fiber and gut microbes play an important role in improving sow performance, a lot of data are still needed to explain the regulation mechanism in the future.

Author contributions

Min Tian and Shihai Zhang initiated the idea, scope, and outline of this review paper. Min Tian, Shihai Zhang, Jiaxin Liu, and Fang Chen studied and analyzed all of the publications cited in this paper and prepared the initial manuscript. Shihai Zhang and Wutai Guan made the final revision. All authors read and approved the final manuscript.

Conflict of interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

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