

Regulation of Poultry Intestinal Health by Dietary Fiber and Mechanisms of Action: Postprint

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Date: 2017-10-11T00:00:00+00:00

Abstract

In recent years, the clinical overuse of antibiotics has greatly reduced the antimicrobial efficacy of these drugs, and antibiotic misuse can also lead to increased colonization of harmful bacteria, affecting the health of humans and animals. Consequently, many countries have begun to prohibit the use of antibiotics as feed additives, and the addition of low-dose antibiotics to feed as intestinal microecological regulators is no longer favored. Therefore, searching for new antibiotic alternatives to regulate the intestinal microbiota of livestock and poultry and maintain intestinal health has become extremely important. Dietary fiber has long been mistakenly considered an antinutritional factor, with claims that fiber can dilute dietary energy levels and affect poultry production performance. However, recent studies have demonstrated that adding appropriate amounts of fiber to poultry diets is an effective nutritional regulation strategy for improving poultry gut health and reducing intestinal disorders. This article reviews the effects of dietary fiber on the regulation of poultry gut health from the perspectives of intestinal development, intestinal mucosal morphology and epithelial tissue health, intestinal digestive physiology, and intestinal microbiota, providing a reference for further research on the regulatory mechanisms of fiber on poultry gut health and offering a scientific basis for the future addition of fibrous substances to poultry diets.

Full Text

Dietary Fiber Regulation of Poultry Gut Health and Its Mechanisms

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Abstract

The long-term and extensive use of antibiotics for medical and veterinary purposes has led to a significant reduction in antimicrobial effectiveness. Antibiotic abuse also promotes colonization by harmful bacteria, threatening both human and animal health. Consequently, many countries have banned antibiotics as feed additives, and the use of low-dose antibiotics as intestinal microecological regulators is no longer acceptable. Identifying alternatives to antibiotics for regulating livestock gut microbiota and maintaining intestinal health has become critically important. Dietary fiber has traditionally been misunderstood as an antinutritional factor that dilutes dietary energy levels and impairs poultry performance. However, recent research demonstrates that appropriate dietary fiber supplementation effectively improves gut health and reduces intestinal disorders in poultry. This review synthesizes current knowledge on how dietary fiber influences poultry gut health across multiple dimensions: intestinal development, mucosal morphology and epithelial tissue health, digestive physiology, and gut microbiota. We aim to provide a reference for further mechanistic studies and scientific guidance for the practical application of fiber supplementation in poultry diets.

Keywords: dietary fiber; digestive tract development; intestinal mucosa; intestinal microecology; poultry; regulation

Recent research has revealed that long-term antibiotic supplementation in livestock feed poses serious threats to human health and environmental safety. Clinical abuse of antibiotics severely disrupts the microecological balance in animal intestines and promotes the emergence of drug-resistant strains. Antibiotic residues in animal products further compromise food safety, while the destruction of gastrointestinal flora creates opportunities for pathogenic bacteria to invade, leading to secondary infections that ultimately affect human health [1]. Many countries have consequently banned or strictly restricted antibiotic use in livestock feed, mandating withdrawal periods [2]. In 2006, European nations legally prohibited all antibiotic use in animal feed. With low-dose antibiotics no longer acceptable as gut microecological regulators, identifying novel alternatives to modulate gut microbiota and maintain intestinal health represents an urgent priority in the post-antibiotic era. This challenge has given rise to the concept of “disease-resistant nutrition,” which recognizes that nutrition influences animal health through multiple pathways: immune function modulation [3], regulation of gut development and microenvironment [2], and impacts on disease onset and progression. Nutritional strategies to regulate gut health and maximize innate immune function are therefore crucial for maintaining animal health, improving performance, and ensuring product safety [2,4]. Against this backdrop, dietary fiber has emerged as a hot topic in poultry nutrition research, particularly regarding its roles in promoting intestinal development, regulating gut microecology, and improving animal welfare.

1 Overview of Dietary Fiber

The term “dietary fiber” first appeared in 1953, initially referring to cellulose, hemicellulose, and lignin [5]. In 1976, Trowell [6] defined fiber as “the indigestible plant cell wall residues that cannot be hydrolyzed by human digestive enzymes.” Although widely accepted by nutritionists, this definition has limitations because some non-cell-wall substances also resist enzymatic digestion. Cummings [7] subsequently proposed that fiber should encompass all non-starch polysaccharides and lignin—a less restrictive definition. In 1984, Asp et al. [8] defined dietary fiber compositionally as including cellulose, hemicellulose, lignin, pectin, gums, and mucilages, while excluding indigestible proteins and lipids, insoluble starch, inorganic elements, waxes, cutin, silicates, and polyamines.

Lu Dexun [9] further elaborated that dietary fiber comprises a complex of components with specific nutritional and physiological functions, where the individual components’ effects do not equal the collective physiological role of fiber. Dietary fiber should include both structural and non-structural fractions, reflect fiber quality, and utilize available indicators rather than crude measures. Analytical methods should comprehensively capture these three definitional aspects while being simple, practical, rapid, and reproducible. Currently, dietary fiber is defined as feed components indigestible by animal endogenous enzymes, primarily plant cell wall constituents including polysaccharides, oligosaccharides, lignin, and related plant substances. Based on solubility, dietary fiber is classified as soluble dietary fiber (SDF) or insoluble dietary fiber (IDF). SDF mainly includes pectin, gums, and some hemicelluloses, which delay gastrointestinal emptying due to high water-holding capacity and viscosity. IDF mainly includes cellulose, hemicellulose, and lignin, which have less impact on stomach and small intestine activity, while their chemical composition, structure, and degree of lignification significantly affect large intestinal fermentation activity and short-chain fatty acid (SCFA) absorption [10].

Following the 1970s, high-energy, high-protein, low-fiber poultry diets dramatically improved production efficiency. Dietary fiber was consequently misperceived as an antinutritional factor that diluted dietary energy, reduced nutrient digestibility, decreased feed intake, and impaired poultry performance [11-12]. For decades, fiber content was minimized in poultry diets, with maximum crude fiber (CF) limits set at <7% for adult broilers and <3% for broiler chicks [13]. However, rising consumer demands for product quality and animal welfare concerns have refocused attention on dietary fiber’ s role in gut health [14]. Recent poultry research confirms that adequate dietary fiber is essential for normal gizzard function, intestinal physiology, microbiota balance, and welfare improvement [11,15-16].

2 Dietary Fiber and Poultry Gut Health

Maintaining gut health is a complex process dependent on delicate equilibrium among diet, gut microbiota, and mucosa (including intestinal epithelial cells and

adherent mucus). Fiber's interactions with intestinal mucosa and microbiota effectively prevent enteric diseases and improve gut health [2,17]. Poultry gut health directly impacts overall health and productivity, and appropriate dietary fiber levels can enhance performance by modulating intestinal development, mucosal morphology, and microecology [18-19].

2.1 Effects of Dietary Fiber on Intestinal Mucosal Morphology and Development

The intestinal mucosa serves as the primary site for nutrient absorption and the first immune barrier between internal and external environments. Maintaining its structural and functional integrity is crucial for poultry gut health and productivity. Current evidence indicates that moderate fiber levels improve intestinal development and mucosal morphology [20].

2.1.1 Effects on Intestinal Mucosal Morphology Cassidy et al. [21] investigated the effects of 15% dietary fiber from alfalfa, wheat bran, cellulose, and pectin on mucosal morphology in mouse jejunum and colon. Fiber altered intestinal mucosal architecture, causing epithelial cell swelling, disorganized villi arrangement, and brush border microvilli shedding. Jamroz et al. [22] reported that beet pulp supplementation elongated colonic villi in geese, while high proportions of hulled oats increased intestinal mucosal thickness. Oats, beet pulp, and grass meal—rich in hemicellulose and cellulose—increased intestinal wall thickness and muscular layer thickness in both small and large intestines. Although fiber sources did not affect villus morphology in the duodenum, jejunum, or ileum, they influenced cecal mucosal morphology without causing morphological damage to intestinal villi [23]. Studies with Gushi chickens fed alfalfa meal as a fiber source demonstrated that increasing dietary fiber levels enhanced villus height and reduced crypt depth without compromising mucosal integrity, indicating that fiber stimulates intestinal development and increases villus length [24]. Li et al. [25] examined the effects of *Leymus chinensis* and corn straw on gut morphology in geese, finding that both fiber sources increased villus height-to-crypt depth ratios in small intestinal segments, with ileal ratios lower than duodenal and jejunal values. The *Leymus chinensis* group showed superior morphological development in the duodenum and jejunum compared to the corn straw group.

Zhu et al. [26] fed Yangzhou geese diets containing alfalfa meal or rice hulls, observing that rice hulls significantly reduced villus height across all intestinal segments at 14 days of age, though differences diminished by 28 days. Due to its high lignification, rice hulls were detrimental to small intestinal villus development, though geese appeared to adapt over time. Alfalfa meal groups exhibited higher villus heights and duodenal lamina propria thickness than rice hull groups, though differences were not statistically significant. Sadeghi et al. [12] fed broilers diets containing 30 g/kg beet pulp, rice hulls, or their combination. At 21 days, beet pulp significantly reduced duodenal and ileal villus heights

compared to controls, while rice hulls and the combination showed no significant differences in villus height, crypt depth, or villus-to-crypt ratios across the duodenum, jejunum, and ileum.

Moderate fiber levels stimulate intestinal motility, promoting orderly villus arrangement, improving mucosal morphology, and accelerating digesta passage, thereby preventing pathogen adhesion to the intestinal wall. Additionally, fiber fermentation produces volatile fatty acids that lower local intestinal pH, inhibiting harmful bacteria such as *E. coli* and *Salmonella* and protecting mucosal structure from damage by bacterial metabolites [27]. These findings indicate that fiber's effects on poultry intestinal morphology depend heavily on fiber type. SDF increases digesta viscosity and content, altering mucosal structure and damaging villus cells, causing atrophy. Conversely, appropriate levels of low-lignification IDF enhance crypt cell proliferation, increase villus length, and improve mucosal morphology, possibly through SCFA production—particularly butyrate—though the precise mechanisms require further investigation.

2.1.2 Effects on Intestinal Development Dietary fiber influences the length, weight, and volume of poultry digestive organs, with effects varying by fiber type, level, and source. Jiménez-Moreno et al. [18] fed broilers diets containing 30 g/kg cellulose, beet pulp, or oat hulls. Beet pulp increased relative intestinal weight compared to controls and cellulose, while oat hulls significantly increased relative gizzard weight compared to beet pulp. Both oat hull and beet pulp groups showed higher relative gizzard weights than controls and cellulose groups, though effects on proventriculus and ceca were not significant. Appropriate oat hull and beet pulp levels enhanced gizzard activity and reduced upper gastrointestinal pH. Pasture feeding or high-fiber diets stimulated gastrointestinal development, particularly increasing gizzard and cecal weights and mucosal thickness [28-29]. Zhou [30] reported that increasing dietary fiber levels in geese increased digestive organ weights, relative weights, and intestinal segment lengths, with highly significant differences in gizzard, proventriculus, duodenum, jejunum, ceca, and rectum. Moderate fiber also promoted small intestinal villus development.

Jiménez-Moreno et al. [31] investigated 5% dietary beet pulp or oat hulls in broilers, finding that fiber significantly increased relative gizzard weight and content while reducing digesta pH. Sacranie et al. [32] demonstrated that oat and barley hulls increased broiler gizzard weight and volume while significantly lowering gizzard pH. Noy et al. [33] showed that rice hulls as an IDF source reduced duodenal relative weight, while beet pulp—rich in pectin—increased intestinal content and small intestinal weight. Sadeghi et al. [12] observed that rice hulls reduced broiler duodenal weight, whereas beet pulp increased jejunal and ileal weights, likely due to pectin increasing viscosity and slowing digesta passage—consistent with reports by Noy et al. [33] and Iji et al. [34] that high SDF levels increase small intestinal weight. Jiménez-Moreno et al. [35] found beet pulp produced longer intestines in 6-12-day-old chicks compared to rice

hulls, while Saki et al. [36] reported that high SDF levels reduced ileal length in 14-day-old broilers.

These studies demonstrate that fiber' s effects on intestinal development depend on fiber type and solubility. SDF increases digesta viscosity, prompting compensatory increases in jejunal and ileal weight to accommodate slower passage rates. IDF increases muscular layer thickness in small and large intestines. However, long-term feeding of highly lignified IDF may be detrimental, potentially damaging epithelial microvilli and reducing nutrient absorption, though this requires further investigation.

2.1.3 Effects on Intestinal Volatile Fatty Acids Dietary fiber fermentation by intestinal microorganisms produces volatile fatty acids, primarily acetate, propionate, butyrate, lactate, and succinate. These SCFAs serve as the main energy source for large intestinal mucosa. In growing and adult pigs, SCFAs provide 15-24% of net energy maintenance requirements, while in humans they supply 5-10% [37-38]. In broilers, large intestinal fermentation contributes 3-4% of metabolizable energy [39]. SCFAs are crucial for non-ruminant gut health: acetate is transported to the liver for muscle energy metabolism; propionate is converted to glucose in the liver; butyrate plays a vital role in maintaining gut health by stimulating epithelial cell proliferation and promoting villus development. SCFAs also enhance water and sodium absorption in the large intestine, preventing diarrhea [2].

Research indicates that increasing dietary fiber levels reduces butyrate proportion while minimally affecting other fatty acids [40]. In broilers, increased IDF significantly elevates butyrate concentration while decreasing acetate relative concentration [41]. Kalmendal et al. [42] fed broilers diets containing high-fiber sunflower cake (37.03% CF, 31.7% IDF) at 0%, 10%, 20%, or 30% inclusion levels (providing 2.30%, 5.42%, 7.96%, and 10.99% dietary CF, respectively). Increasing IDF linearly decreased jejunal acetate and propionate contents, with no significant differences in butyrate. Lactate content also tended to decrease with higher IDF levels. Fiber type influences SCFA composition, as high SDF levels may increase microbial populations and total SCFA production [40]. The acidic environment created by SCFAs inhibits colonization of pathogenic bacteria such as *E. coli*, *Salmonella*, and *Clostridium* [20]. SCFAs also induce mucin and trefoil factor secretion, improving mucus layer viscoelastic properties, reducing inflammatory cell infiltration, participating in mucosal maintenance and repair, promoting villus development, and enhancing mineral absorption [43-44].

Current literature on dietary fiber' s effects on poultry SCFA production is limited and inconsistent, likely due to variations in fiber source, solubility, and inclusion level. Compared to ruminants, poultry show specific responses: increased dietary fiber tends to decrease acetate and propionate, slightly reduces lactate, and either increases or does not affect butyrate. Future research should investigate mechanisms underlying fiber' s effects on SCFA production and utilization, particularly butyrate' s role in promoting villus and mucosal development.

2.2 Effects on Digestive Physiology

2.2.1 Effects on Intestinal Motility Appropriate fiber types help maintain normal gastrointestinal motility, enzyme secretion, and intestinal pH. IDF enhances intestinal motility by absorbing water and sustaining normal digestive tract activity, while stimulating colonic motility. Intestinal peristalsis moves small intestinal contents into the ceca, and reverse peristalsis allows rectal contents to reflux into the ceca. Slow cecal motility and reverse peristalsis ensure thorough mixing of contents, creating optimal conditions for microbial fermentation [45]. Shi et al. [46] studied digesta passage rates of five feed types in ducks, finding the following order from fastest to slowest: *Hemarthria compressa* > wheat bran > rapeseed meal > soybean meal > corn, demonstrating that higher dietary fiber accelerates digesta passage. Different fiber types exert distinct effects on motility [47]. Unfermented fiber fractions mechanically influence motility and digesta retention, while fermentable fractions may affect motility through fermentation products. Further research is needed to elucidate mechanisms by which different fiber sources influence intestinal motility to provide scientific guidance for gut health regulation.

2.2.2 Effects on Digestive Enzymes Dietary fiber affects activities of amylase, trypsin, chymotrypsin, and lipase in the stomach and small intestine, with impacts varying by fiber source, inclusion level, and enzyme type. High-fiber diets influence digestive enzyme activity and digestive juice secretion, causing physiological and morphological changes that increase endogenous losses of protein, lipids, electrolytes, and water [48], resulting in enlarged digestive organs, increased secretions, and reduced nutrient absorption. Barley supplementation in broiler diets significantly reduced intestinal lipase and amylase activities, while high-fiber diets increased endogenous secretions of protein, lipids, and electrolytes [45]. Mosenthin et al. [49] found that pectin did not significantly affect pancreatic enzyme or juice volume but reduced pancreatic α -amylase secretion. Fiber may reduce enzyme activity by binding enzymes and preventing substrate interaction. Diets containing alfalfa meal and pectin increased cecal amylase and cellulase activities, likely because non-starch polysaccharides and undigested starch fermented in the ceca, promoting microbial growth and enzyme production [50]. Wang et al. [51] reported that high wheat bran levels in broiler diets reduced pepsin, total intestinal protease, and amylase activities, while increasing trypsin activity—possibly due to SDF-induced pancreatic compensatory hypertrophy and increased enzyme secretion. In Gushi chickens fed alfalfa meal, cecal cellulase activity increased significantly with dietary fiber level and age, as appropriate fiber fermentation produced SCFAs that promoted microbial proliferation and cellulase production [24].

Current research on fiber's effects on digestive enzyme secretion shows inconsistencies likely related to fiber source, level, and type. Highly lignified, high-fiber diets may reduce enzyme secretion and activity, increasing endogenous nutrient losses. Conversely, appropriate levels of low-lignification fiber can stimulate

enzyme activity, particularly cellulase.

2.2.3 Effects on Intestinal pH Intestinal pH is primarily regulated by neural and hormonal factors, but is also influenced by age and diet. Dietary fiber affects pH at different intestinal sites. In 21-day-old broilers fed wheat- and sorghum-based diets, pH values were: crop 4.82-4.98, proventriculus 3.12-3.78, gizzard 2.61-2.67, small intestine 5.29-5.78, and ceca 4.80-5.12 [52]. Jiménez-Moreno et al. [18] reported that oat hulls and beet pulp reduced gizzard pH compared to cellulose, possibly by stimulating hydrochloric acid secretion in the proventriculus. Few studies have examined fiber' s effects on intestinal pH, though fiber does not significantly affect duodenal pH. pH decreases progressively from duodenum to jejunum, with greater reductions for cellulose than beet pulp. These findings indicate that fiber primarily affects gizzard pH, significantly lowering it—likely by stimulating acid secretion in the proventriculus. Further research is needed to investigate mechanisms underlying fiber' s effects on intestinal pH.

2.3 Effects on Intestinal Microecology

A balanced gut microecology is essential for poultry health and performance. Dietary fiber influences microbial diversity, with appropriate fiber levels providing favorable conditions for proliferation [2]. Moderate fiber significantly increases *Lactobacillus* populations in goose intestines [53]. Wang et al. [54] reported that increasing dietary fiber linearly increased *Bifidobacterium* and *Lactobacillus* numbers in geese. Shao et al. [28] found that supplementary green forage enhanced cecal microbial activity, while appropriate fiber levels provided a barrier effect, inhibiting pathogenic microorganisms such as *Clostridium* and *Salmonella typhimurium*, thereby improving gut microecology and health [55]. Shakouri et al. [56] demonstrated that 3% citrus pectin in broiler diets increased small intestinal digesta viscosity, slowed passage rate, and elevated cecal Enterobacteriaceae.

SDF, poorly digested by poultry enzymes, serves as a microbial fermentation substrate in the lower digestive tract, producing SCFAs that stimulate proventriculus hydrochloric acid secretion. This synergistic action lowers intestinal pH, inhibiting harmful bacteria like *Salmonella* while not affecting beneficial *Lactobacillus* [57]. In Gushi chickens fed alfalfa meal, increasing dietary fiber (2.51-7.79%) significantly increased cecal microbial diversity and abundance, promoting proliferation of fiber-degrading *Clostridium cellulolyticum*, *Prevotella*, carbohydrate-fermenting *Bacteroides*, and *Clostridium* spp. [24]. Hu et al. [55] fed geese diets containing *Pennisetum purpureum*, finding that *Lactobacillus* counts increased with crude fiber levels (5.03-8.98%), but declined at 10.98% crude fiber along with *E. coli*. Wang et al. [58] reported that in Jilin white geese fed diets based on *Leymus chinensis* or corn straw, microbial colonization was complete by day 46. The corn straw group showed higher bacterial numbers, while the *Leymus chinensis* group had higher relative abundances of

Lactobacillus and *Bifidobacterium*. *E. coli* dominated the proventriculus, *Enterococcus* and *Lactobacillus* dominated the ileum, and *Staphylococcus*, *Bacteroides*, *Eubacterium*, *Bifidobacterium*, and *Peptococcus* dominated the ceca.

Jiménez-Moreno et al. [31] investigated 5% oat hulls or beet pulp in broilers, finding that beet pulp increased crop *Lactobacillus* numbers while oat hulls did not; neither fiber source affected cecal *Lactobacillus*. IDF sources like oat hulls improved gizzard function and mechanically stimulated gastrointestinal mucosa, enhancing motility and reducing adhesion opportunities for pathogenic *Clostridium perfringens*. Kalmendal et al. [42] reported that 20% sunflower cake reduced *Clostridium* spp. compared to controls, while 10% sunflower cake reduced *Lactobacillus* spp., with no significant differences in *E. coli*. Liu [59] examined rice hull effects on Yangzhou geese, finding that 20% and 40% rice hull diets promoted cellulolytic and carbohydrate-fermenting bacteria including *Clostridium*, *Cellulomonas*, *Bacteroides*, *Treponema*, and *Eubacterium*. Increasing fiber levels elevated *Lactobacillus*, *Veillonella*, and *Clostridium* cluster IV while reducing *E. coli*, though *Bifidobacterium* was unaffected. However, excessive fiber (60% rice hulls) increased cecal *E. coli* and Enterobacteriaceae.

These results demonstrate that gut microbial composition is influenced by fiber source, solubility, lignification, and inclusion level. SDF increases microbial numbers and diversity in the large intestine and ileum, while IDF enhances motility, reducing pathogen adhesion to mucosal surfaces (e.g., *C. perfringens*). Due to slower degradation, IDF primarily ferments in the large intestine, affecting microbial populations there. Early research was limited by culture-dependent methods focusing on easily cultivated bacteria like *E. coli*, *Salmonella*, and *Lactobacillus*. The complex poultry gut microbiome can now be characterized using culture-independent molecular techniques such as PCR-DGGE, enabling rapid and accurate assessment of fiber' s effects on microbial communities.

Beyond genetic and environmental factors, nutrition is the primary determinant of gut health. Dietary fiber manipulation represents a novel nutritional strategy for regulating poultry gut health. Appropriate fiber levels promote intestinal development, improve microvilli structure, reduce pH, and enhance microecology. However, fiber' s regulatory effects constitute a complex process involving intestinal epithelial cells, mucus, and microbiota. Current research shows inconsistencies, with most studies focusing on geese rather than broilers or laying hens. Systematic investigations are lacking. Future research should systematically examine mechanisms by which different fiber sources regulate overall gut health and establish optimal fiber requirements for maximal performance and gut health, providing scientific guidance for effective fiber utilization in poultry production.

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