

Role of Carbohydrate Digestion in Equids in Maintaining Cecal Microbiota Stability and Host Health (Postprint)

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Abstract

The cecum of equids harbors a complex and diverse microbiota that plays a crucial role in the digestion of dietary carbohydrates and in maintaining host health, thereby forming the foundation of cecal function in these animals. Concurrently, dietary carbohydrates also influence the cecal microbiota. Investigating the digestive metabolism of dietary carbohydrates within the cecum and their effects on, as well as the patterns of influence upon, the cecal microbiota holds significant guiding value for feed production, animal husbandry, and the enhancement of animal production performance. This review summarizes the characteristics of the cecal microbiota, its status and role in the carbohydrate digestive physiology of equids, and the digestive physiology of carbohydrates in the equid cecum. It further provides an analytical overview focusing on the effects of dietary carbohydrates on the cecal microbiota of equids and the underlying patterns, along with the current research status and advances in nutrition-related metabolic diseases associated with carbohydrate digestion in the equid cecum.

Full Text

Roles of Equine Carbohydrate Digestion in the Maintenance of Cecal Microbial Stability and Host Health

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Abstract: The cecum of equine animals harbors complex and diverse microorganisms that play a crucial role in dietary carbohydrate digestion and host health, forming the foundation of cecal function. Concurrently, dietary carbohydrates also influence cecal microbial populations. Investigating the digestive metabolism of dietary carbohydrates in the cecum and their effects on cecal microbial flora holds significant guiding value for feed production, animal feeding practices, and improvements in animal production performance. This review summarizes the characteristics of cecal microorganisms, their roles in equine carbohydrate digestive physiology, and the carbohydrate digestive physiology in the equine cecum, with particular emphasis on analyzing the effects and patterns of dietary carbohydrates on equine cecal microbial flora, as well as the current research status and advances in nutrition-related metabolic diseases associated with cecal carbohydrate digestion.

Keywords: equine; cecum; microorganism; carbohydrates; physiology of digestion

Equine animals primarily include horses, donkeys, and mules, all of which are traditional livestock species in China. As a major horse-raising country, China not only possesses rich breed resources but also ranks first worldwide with approximately 9 million horses in inventory [?]. Additionally, China has the largest donkey population and most diverse breed resources globally, with about 6 million donkeys at the end of 2013 [?]. The cecum serves as a vital organ for nutrient digestion in equine animals and represents the primary site for microbial digestion of dietary fiber. Carbohydrates that cannot be digested and absorbed in the stomach and small intestine (such as cellulose and starch) play a decisive role in maintaining cecal microbial flora and cecal environment stability, ultimately affecting feed utilization efficiency, nutrient metabolism, and animal production performance. For a long time, research on equine animals has been undervalued in China's animal science field, resulting in limited understanding of their feeding, nutrition, digestion, and metabolism. This review focuses on the relationship between cecal microorganisms and carbohydrate digestion in equine animals, synthesizing the latest international research progress to provide insights and methodological inspiration for Chinese researchers.

1. Cecal Carbohydrate Digestion in Equine Animals

Equine animals are typical monogastric herbivores with a hindgut fermentation pattern. Their digestive tract anterior resembles that of typical monogastric

animals, while the posterior segment, including the cecum and colon, is voluminous and hosts massive, diverse microbial populations similar to the rumen of ruminants, playing an important role in microbial digestion and metabolism of dietary carbohydrates. Energy sources for equine animals primarily include glucose and volatile fatty acids (VFAs), with glucose derived from starch breakdown in the small intestine and VFAs produced through microbial fermentation of fiber in the cecum. Approximately 60-70% of the energy required by equine animals is provided by VFAs absorbed from the cecum and colon [?].

1.1. Cecal Digestion of Starch and Fiber

Arnold et al. [?] found that the digestibility of cereal starches such as corn, oats, barley, and sorghum in the equine cecum could reach $(91.1 \pm 6.8)\%$. Starch that escapes digestion in the anterior digestive tract is converted to lactic acid by lactic acid-producing bacteria such as *Streptococcus bovis* and *Lactobacillus* sp. in the hindgut [?], which is subsequently transformed into propionic acid by lactic acid-utilizing bacteria like *Veillonella* spp. [?]. This propionic acid is then absorbed through the cecal wall to provide energy for the host. When horses are fed forage or silage, most fiber is digested in the cecum and colon. Miyaji et al. [?] reported that fiber digestion in the cecum accounts for approximately 90% of total fiber digestion in the entire digestive tract, with strong activities of carboxymethyl cellulase and xylanase detected in the cecum. Glinsky et al. [?] demonstrated that microorganisms in the equine hindgut hydrolyze cellulose and hemicellulose from fescue grass to release soluble sugars, which are then fermented into VFAs including acetate, propionate, and butyrate (in a ratio of 7:2:1). These VFAs, absorbed through the cecal wall, can provide 30% of digestible energy, particularly when horses consume high-fiber diets where fiber fermentation becomes the primary energy source.

The microbial fermentation mechanism of fiber in the equine cecum is quite similar to that in the rumen of ruminants, though utilization efficiency differs. Hintz et al. [?] found that the efficiency of plant cell wall component utilization in monogastric herbivores with hindgut fermentation is only about two-thirds that of ruminants. However, Izraely et al. [?] observed that donkeys digest hay energy as efficiently as ruminants.

1.2. Factors Affecting Cecal Carbohydrate Digestion

Cecal function is primarily fiber digestion, which is mainly influenced by feed intake, diet composition, and feeding management. Feed intake and diet composition first affect the amount and composition of fermentable substrates reaching the cecum while also influencing digesta retention time in the digestive tract, ultimately affecting fiber digestibility in the cecum. Miyaji et al. [?] reported that the mean retention time of timothy hay in the equine cecum was 2.9 hours. When horses are fed silage, the mean retention time of both liquid and solid phases throughout the digestive tract is shorter than when fed hay (16.9 h vs. 21.1 h; 21.8 h vs. 23.7 h) [?]. Furthermore, higher proportions of small parti-

cles in the diet prolong retention time [?]. Numerous studies have demonstrated that extended retention time increases nutrient digestibility, microbial activity, and water absorption from the digestive tract [?].

The cecum possesses a unique anatomical structure, being sac-like and rich in fluid. When feed intake increases, the cecum becomes well-filled, preventing digesta from the ileum from entering the cecum and instead directing it straight to the colon. Dry matter intake in horses is generally about 2% of body weight [?], and high intake reduces total tract fiber digestibility and mean retention time, indicating a direct relationship between fiber digestibility and retention time [?]. Additionally, the ratio of structural to non-structural polysaccharides in the diet affects cecal digestive function. If the starch proportion in equine diets is too high, exceeding 3.5 g/kg BW, cecal pH decreases, reducing cecal polysaccharidase activity and consequently fiber digestibility [?].

2. Equine Cecal Microorganisms

Fiber fermentation plays a critical role in equine digestion, including maintaining cecal environment stability and providing energy for the host—functions that depend entirely on the presence of cecal microorganisms, which thus form the foundation of cecal function. The degradation and fermentation of fiber into absorbable nutrients by microorganisms represent the primary function of the equine intestinal ecosystem [?]. Although cecal fermentation closely resembles rumen fermentation in terms of microbial digestion, secretion, and absorption, research on equine cecal fermentation remains inadequate, and studies on hindgut microbial diversity are particularly scarce.

2.1. Microbial Composition

Compared to the rumen of ruminants and the cecum and colon of humans and pigs [?], knowledge of donkey cecal microbial populations is extremely limited, with only sporadic reports available. In contrast, research on horse cecal microorganisms is more extensive. The equine cecum maintains a near-neutral pH and slow flow rate, providing a favorable environment for microorganisms [?]. The cecal microbiota comprises bacteria, fungi, and protozoa [?], though most research has focused on cecal bacteria. Santos et al. [?] estimated that 30–80% of microorganisms in the equine cecum are strict anaerobes, with total anaerobic bacterial counts ranging from 1.85×10^7 to 2.65×10^9 CFU/mL. Fungal spore counts range from 10^1 to 10^4 CFU/mL [?], while protozoal counts range from 10^3 to 10^5 cells/mL [?].

2.1.1. Bacteria Cecal bacteria are predominantly anaerobic, outnumbering the animal's own cells and significantly impacting nutrition and health [?]. Bonhomme [?] identified three major fiber-degrading bacteria in pony intestines using morphological methods: *Fibrobacter*, *Ruminococcus*, and *Ruminococcus*

albus. Milinovich et al. [?] detected *Streptococci* and *Saccharomyces cerevisiae* in the equine cecum. Jouany et al. [?] identified *Lactobacilli*, *Ruminococcus flavefaciens*, and *Fibrobacter succinogenes* as fiber-degrading bacteria.

Traditional microbial cultivation methods can only capture partial information about the intestinal environment and isolate a limited fraction of microorganisms—estimated at only 10–20% [?]-with most isolates belonging to common genera, preventing comprehensive and objective understanding of intestinal microbial communities. Modern microbial technologies have opened new effective avenues for analyzing cecal digestion mechanisms from a microbial perspective. Molecular methods such as nucleic acid sequence analysis and genotypic fingerprinting overcome the limitations of cultivation methods. Ribosomal RNA (rRNA) small subunits are widely recognized as excellent molecular clocks and represent the most commonly used method for elucidating microbial phylogenetic relationships. Recent advances in molecular biology have yielded numerous technologies for identifying unculturable microorganisms, including 16S rDNA clone library sequencing and genotypic fingerprinting. Real-time quantitative PCR enables precise and sensitive quantification of individual species or total bacterial counts [?].

Hastie et al. [?] used real-time quantitative PCR to identify *Ruminococcus flavefaciens* as the most abundant species in equine cecal contents, followed by *Fibrobacter succinogenes*, with *Streptococcus bovis* being the least abundant. Julliard et al. [?] used oligonucleotide probes to detect fiber-degrading bacteria in donkey and pony ceca, finding *Ruminococcus flavefaciens* as the dominant species. Daly et al. [?] employed culture-independent methods to analyze microbial diversity in the cecum of forage-fed horses, revealing that cecal microorganisms primarily belong to Gram-positive anaerobes, mainly *Lachnospiraceae* from the phyla *Bacteroidetes* and *Firmicutes*, followed by *Fibrobacter*, *Ruminococcaceae*, and *Bacillus*, *Lactobacillus*, and *Streptococcus* from *Firmicutes*.

2.1.2. Protozoa Kornilova et al. [?] investigated ciliates in Yakut horse intestines, identifying 57 species with an average of 17–43 species per horse. Julliard et al. [?] examined the population structure and distribution of large intestinal ciliates in 15 Turkish horses, identifying 36 species across 22 genera, with average ciliate counts of $(4.2 \pm 13.9) \times 10^4$ cells/mL and an average of (9.9 ± 7.1) species per host. While the contribution of rumen protozoa to digestion has been extensively studied, few reports address the role of protozoa in equine hindgut digestion. Moore et al. [?] and Gürelli et al. [?] also detected ciliates in the equine cecum and colon, suggesting that protozoa appear unimportant for fiber digestion.

2.2. Effects of Dietary Carbohydrates on Cecal Microorganisms

The efficiency of hindgut fermentation depends on available substrates and is influenced by feed intake, diet composition, and pre-cecal digestion [?].

2.2.1. Dietary Carbohydrate Ratios Medina et al. [?] reported that equine intestinal microbial composition and activity are affected by dietary fiber-to-starch ratios. To maintain normal intestinal microflora and ensure hindgut health, dietary starch must be balanced with equivalent fiber, specifically a dietary neutral detergent fiber (NDF)/starch ratio of 1. Studies show that dietary changes alter equine cecal microbial flora. Goodson et al. [?] measured changes in cecal microbial populations during an abrupt dietary shift from all-forage to all-concentrate, finding that microbial population changes correlated with this sudden transition. When dietary starch exceeds 0.4% of body weight, some starch escapes small intestinal hydrolysis and reaches the cecum, where fermentation produces lactic acid and carbon dioxide [?]. Lactic acid dramatically reduces cecal pH, inhibiting fiber-degrading bacterial activity and disrupting normal cecal microflora. Conversely, adequate dietary fiber maintains fiber-degrading bacterial activity, with high-fiber diets showing higher fiber digestibility compared to high-starch diets [?].

2.2.2. Carbohydrate Types Generally, most non-structural carbohydrates either fail to reach the hindgut or arrive only in minimal amounts, whereas structural carbohydrates, poorly digested pre-cecally, continue to be hydrolyzed in the hindgut. For instance, increasing dietary grain concentrate proportions to raise starch content above 2 g/kg BW [?] can decrease cecal pH to 6.1 [?], negatively impacting microbial activity and fiber digestion. Cecal microbial proliferation and crude fiber digestion depend on available energy [?], and different carbohydrate types and intake levels affect retention time in the digestive tract, consequently influencing hindgut microbial composition [?]. Starch fermentation in the hindgut induces unfavorable changes in microbial flora and activity, either reducing dietary digestibility or severely compromising animal health. These microbial population shifts may relate to substrate competition among equine cecal microorganisms, though no relevant studies have been reported to date.

2.2.3. Yeast Additives and Antibiotics Beyond conventional feeds and nutrients, additives such as live yeast, grape seed extract, and antibiotics also affect cecal microorganisms. Glade et al. [?] found that supplementing equine diets with live yeast (10 g/d) increased cecal anaerobic bacterial counts and optimized cecal fermentation patterns. Research shows that yeast promotes the growth of lactic acid-utilizing bacteria and fiber digestion while tending to increase their populations [?]. Antibiotics such as virginiamycin are commonly used to treat carbohydrate-induced laminitis in horses by preventing abnormal *Streptococcus* growth, reducing cecal lactic acid production, and maintaining cecal pH above 6.5 [?].

3. Cecal Carbohydrate Digestion and Host Health

While diets influence cecal microorganisms, microbes also exert beneficial or detrimental effects on the host. Fiber-based diets maintain normal cecal fermentation conditions, whereas high-concentrate diets disrupt the cecal environment, leading to metabolic disorders such as acidosis and laminitis [?]. Starch that escapes pre-cecal digestion alters cecal microbial flora and produces metabolites that ultimately cause digestive diseases in horses.

Intestinal disorders such as colic significantly impact equine health and often cause death. The direct cause of colic is digestive and absorptive dysfunction leading to intestinal distension and spasms, manifested as severe abdominal pain [?]. Laminitis is another nutrition-related metabolic disease associated with cecal digestion, with extensive research confirming its link to hindgut microbial flora [?]. Milinovich et al. [?] used 16S rRNA sequence analysis to identify *Streptococcus* species in the hindgut of laminitic horses, finding that Gram-positive streptococci associated with carbohydrate-induced laminitis proliferate when large amounts of fermentable starch reach the hindgut.

Dietary fiber plays a crucial role in maintaining hindgut environmental stability and preventing acidosis. Compared to forage-fed horses, concentrate-fed horses exhibit significantly decreased cecal pH (reaching 4–5) six hours post-feeding, with the cecal acetate-to-propionate ratio dropping from 5.0 during hay feeding to 2.6 during concentrate feeding [?]. This pH reduction inhibits hindgut fiber-degrading bacterial activity and increases susceptibility to colic and laminitis.

Research on equine cecal carbohydrate digestive physiology remains far less systematic and thorough than that on ruminant rumen function, and understanding of equine cecal microorganisms is very limited. Moreover, most literature cited herein focuses on horses, with scarce information on donkeys. As a typical equine species, whether donkeys share the same characteristics as horses regarding cecal microorganisms and carbohydrate digestion, or possess unique features due to species and environmental differences, requires further investigation.

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