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The Impact of Diet on the Hindgut Microbiome

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ABSTRACT

In horses, dietary components that are not digested by host enzymes in the foregut pass unchanged through to the hindgut where they have a profound effect on the microbiome. Epidemiologic studies have given evidence that important equine health issues could result from dysbiosis in the hindgut ecosystem as a result of dietary factors. This review presents an outline of plant carbohydrates degradation by the equine hindgut microbiome. Then, data are summarized from studies assessing the variations of the microbiome occurring in the hindgut under different dietary changes. In the literature, most studies examined the impact of abrupt changes and changes between high-starch versus highfiber diets, while the effect of feed form and processing or feeding frequency was rarely explored. Finally, the representativeness of the fecal microbiome changes is compared to the hindgut changes when horses are submitted to dietary changes.

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1. Introduction

In horses like in other species, diet has a profound effect on the microbiome of the hindgut. Dietary components that are not digested by host enzymes in the foregut pass unchanged through to the hindgut and deliver a variety of growth-promoting and growthinhibiting factors which influence the balance between species specialized for the fermentation of different substrates within the microbial community. Nondigestible plant cell wall polysaccharides provide substrates for the growth of fibrolytic microorganisms, which is essential to the host, as they in turn provide energy via the end products of their metabolism, especially short-chain fatty acids (SCFAs).

Epidemiologic studies have given evidence that important equine health issues such as colic [1-7] and laminitis [8,9] could result from dysbiosis in the hindgut ecosystem as a result of dietary factors. Primary data also showed substantial alterations in the hindgut bacteria of horses submitted to abrupt ingestion of concentrate, provoking an acute form of laminitis [10].

The direct study of the hindgut microbiota composition as well as its activity provides a clear picture of the state of the microbial ecosystem balance. Direct studies have been conducted experimentally using cecal and colonic contents collected from fistulated or euthanized horses, but which is not feasible in the field. Using other materials such as feces could provide an easily collected alternative thus enabling the observation of dietary-related variations of the hindgut microbial ecosystem. Fecal data could provide information regarding microbial balance and efficiency of fiber degradation and thus giving insight to prevent the incidence of colic or laminitis.

Along this review, we studied only information that looked specifically at equine. After an outline of plant carbohydrate degraders, we summarized data from studies assessing the variations of the microbiome occurring in the hindgut under different dietary changes. Finally, we discussed the representativeness of the fecal microbiome changes compared to the hindgut ones when horses are submitted to dietary changes.



Review Article





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2. The Hindgut Microbiome and Plant Carbohydrate Degraders

There would be no horse without hindgut microorganisms! Indeed, cell wall carbohydrates (including cellulose, hemicelluloses, and pectins) that represent from 35% to 60% on average in the equine diet contain bonds that are resistant to the horse's hydrolytic enzymes. Only microbial enzymes can break them down in the hindgut, which offers a propitious environment with ideal physicochemical characteristics for microorganisms' growth and fermentative activity.

Dietary starch and water-soluble carbohydrate (WSC) represent from about 10% to 40% of the daily ration [11]. A fraction of this carbohydrate fraction may not be fully digested in the foregut, either due to starch granule structure or to a limited capacity of the amylase or a lack of fructanase in the small intestinal.

In the hindgut plant, carbohydrate degradation involves two steps: first the hydrolysis of complex polysaccharides and second the fermentation of the simple sugars (Fig. 1).

2.1. Complex Polysaccharides Utilizers

The first step of the complex polysaccharides degradation process consists of the attachment of microorganisms to plant cell walls. This adhesion directs concentrated enzymes to the substrates, ensuring hydrolysis of polysaccharides. Enzymes involved in plant cell wall and starch degradation were shown to originate mainly from bacteria bound to particles both in the equine cecum and colon content, rather than from bacteria present in the liquid phase [12].

Fungal species of *Piromyces* genus and bacterial species of the *Ruminococcus* and *Fibrobacter* genera have been identified as major fibrolytic microorganisms responsible for plant cell wall degradation in the equine hindgut. Further detail of those microorganisms involved in dietary plant cell walls degradation and more generally of the equine hindgut microbiome has been published in a recent review [13]. The main amylolytic bacteria identified in the equine hindgut belong to the *Streptococcus* and *Lactobacillus* genera. Some strains have been isolated: *Streptococcus* bovis, *S. equinus*, *Lactobacillus* salivarius, and *L. mucosae* [14–16].

2.2. Simple Sugars Fermenters

Fibrolytic and amylolytic species hydrolyze carbohydrate into simple sugars (cellobiose, glucose, xylose) which are further fermented. The resulting end products of fermentation are SCFAs (most commonly known as volatile fatty acids [VFAs] in herbivores), lactate, and gases (CO₂ et CH₄) (Fig. 1).

The major end product measured after the fermentation of cellobiose by the four cecal strains of Ruminococcus sp. isolated by Julliand et al [17] was acetate, whereas little to no lactate was found. On the contrary, amylolytic bacteria are also called lactic acid producing bacteria as they produce lactate as main end product from starch or WSCs fermentation [15,18,19]. Streptococcus bovis and S. equinus are only L-lactate producers, whereas other strains were reported to produce both isomers of lactate [16]. Lactate is a substrate for lactate-utilizing bacteria, which are able to convert it into VFAs, mainly propionate. The major lactateutilizing bacteria belong to the Veillonellaceae families and to the Megasphaera and Veillonella genera. Peptostreptococcus elsdenii (now Megasphaera elsdenii) and Veillonella gazogenes (now Veillonella alcalescens) were identified early on as main lactate-utilizing bacteria species in the hindgut [18,20].

The global VFA composition within the hindgut content is determined by the microbiota composition and by the nature of plant carbohydrates in the digesta. The activity of fibrolytic microorganisms induces high levels of acetate (C2) and to a lesser extent of butyrate (C4), whereas the activity of amylolytic microorganisms induces a large increase in propionate (C3) proportion. Thus, the fibrolytic activity resulting from plant cell wall fermentation can be evaluated in horses through the ratio [(acetate + butyrate)/ propionate] ([{C2 + C4}/C3]), as it was suggested in

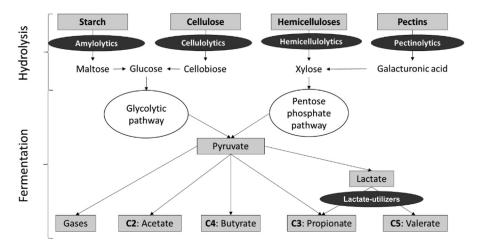


Fig. 1. Pathways of plant complex polysaccharides hydrolysis and fermentation by the hindgut microbiota and resulting end products.

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