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Contents

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Contents

World Journal of Gastroenterology

Weekly Volume 27 Number 45 December 7, 2021

Contents

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Editorial Board Member of *World Journal of Gastroenterology*, Oscar Teramoto-Matsubara, MD, AGAF, FACG, FACP, Associate Specialist, Department of Gastroenterology, ABC Medical Center, Mexico City 11000, Mexico. teramotomd@prodigy.net.mx

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OPINION REVIEW

Humans have intestinal bacteria that degrade the plant cell walls in herbivores

Shunji Fujimori

ORCID number: Shunji Fujimori 0000-0002-6214-2595.

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Shunji Fujimori, Department of Gastroenterology, Chiba Hokusoh Hospital, Nippon Medical School, Chiba 270-1694, Japan

Corresponding author: Shunji Fujimori, AGAF, MD, PhD, Director, Department of Gastroenterology, Chiba Hokusoh Hospital, Nippon Medical School, 1715 Kamagari, Inzai-City, Chiba 270-1694, Japan. s-fujimori@nms.ac.jp

Abstract

The cell walls of plants are mainly made of cellulose and contain a large number of calories. However, the main component, cellulose, is an indigestible plant fiber that is thought to be difficult for humans to use as energy. Herbivores acquire energy through the degradation of cell wall-derived dietary fiber by microorganisms in the digestive tract. Herbivores, especially horses, have a highly developed cecum and large intestine, and plants are fermented for their efficient use with the help of microorganisms. Humans also have an intestinal tract with a wide lumen on the proximal side of the large intestine, in which fermentation occurs. The digestive process of horses is similar to that of humans, and many of the intestinal bacteria found in horses that degrade plants are also found in humans. Therefore, it is thought that humans also obtain a certain amount of energy from cell wall-derived dietary fiber. However, the intake of dietary fiber by modern humans is low; thus, the amount of calories derived from indigestible plant fiber is considered to be very low. Cellulose in the plant cell wall is often accompanied by hemicellulose, pectin, lignin, suberin, and other materials. These materials are hard to degrade, and cellulose is therefore difficult for animals to utilize. If the cell wall can be degraded to some extent by cooking, it is thought that humans can obtain calories from cell wall-derived dietary fiber. If humans can use the calories from the cell wall for their diet, it may compensate for human food shortages.

Key Words: Intestinal flora; Human; Herbivore; Indigestible plant fiber; Cell wall; Calorie

Core Tip: The plant cell wall is mainly composed of cellulose and contains a high number of calories. However, it is classified as an indigestible dietary fiber, and its

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energy utilization is difficult. Many of the intestinal bacteria found in herbivorous horses that degrade plants are found in humans. Therefore, it is thought that humans can also utilize plant cell walls for energy to some extent. If cell wall-derived dietary fiber can be cooked to make it easier for humans to use, it may compensate for human food shortages.

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INTRODUCTION

Cell walls support the structure of plants and are mainly composed of cellulose. Cellulose contains a large amount of potential energy, although only the method of binding glucose molecules makes it different from starch. Therefore, it is beneficial for organisms to use cell walls as energy. However, with the exception of a few multicellular organisms, such as termites, the main organisms that are capable of digesting the cell wall with their own cellulases are microorganisms, and most higher organisms cannot digest the cell wall without the assistance of microorganisms.

Some bacterial groups have enzymes that degrade cell wall components through fermentation, and many herbivores use this fermentation ability in the digestive tract to obtain energy from plant cell walls. Plant digestion is divided into various methods according to the evolution of animals. Many herbivores have a large fermenting organ in their digestive tract, but there are also herbivores, such as giant pandas that eat bamboo as their staple food, that have a digestive tract similar to that of carnivorous animals[1]. Therefore, herbivores do not necessarily need fermenting organs.

Humans are classified as omnivorous animals and eat plants. Plants consumed by humans are utilized *via* the decomposition and absorption of easily available plant cell contents. Most components of the cell wall are classified as indigestible insoluble dietary fibers and are thought to contribute little to the energy of humans. However, in the human intestinal flora, there are many bacterial species that degrade the cell wall that are also found in the gastrointestinal flora of herbivorous animals. Therefore, intestinal bacteria can ferment cell wall components that are classified as insoluble dietary fibers. It is thought that the components degraded by bacteria can be utilized by humans.

The utilization of energy derived from cell walls can improve the increasing eating habits of humans. In this paper, we examine the similarities in intestinal bacteria between humans and herbivores and summarize the findings on the utilization of energy derived from plant cell walls by humans.

CELL WALL DIGESTION

Plant cell walls consist of two layers. The outer layer is formed first and is called the primary cell wall. The primary cell wall is mainly composed of cellulose. Cellulose has a strong molecular bond with glucose, and crystalline cellulose is very hard and wiry. Hemicellulose and pectin are bound to hard wire-like cellulose. Therefore, cellulose is considered to be difficult to degrade. In the secondary cell wall formed at the site where plant growth has stopped, lignin binds to cellulose to increase its strength. Lignin is a polymer that can have completely different structures depending on the plant species and the growing environment. This lignin binds to cellulose and interferes with cellulase action[2]. Furthermore, it is very difficult to degrade cell walls with attached waxy suberin. Cork is rich in suberin and lignin; however, the fact that cork retains its morphology for a long period of time suggests that it is difficult to degrade, even by bacteria.

Moreover, the cell wall is made of hard cellulose solidified with other molecules to further increase its strength. For this reason, a large amount of effort is required to degrade the cell wall. Thus, most organisms do not degrade the cell wall themselves and instead utilize a method to mainly consume cell contents that are easily absorbed.

For example, although butterfly or moth larvae actively eat the leaves of plants, there are few bacteria in their gastrointestinal tracts. They chew the leaves and absorb the cytoplasm in them, and the cell walls are excreted from the body. In other words, except for a few kinds of insects, such as termites, it is difficult even for insects to utilize the cell wall.

If organisms consume a large number of plants, then enough of the contents of the cells can be ingested. However, plant abundance is not always sufficient. Large amounts of plants are required, especially for large herbivorous organisms. Herbivores are animals that use bacteria to degrade plant cell walls to efficiently ingest and digest plants. If the cell wall can be converted into energy, efficient energy intake can be achieved with fewer plants. Herbivores have bacteria in their gastrointestinal tracts that can degrade cell walls. There are several ways in which bacteria degrade the cell wall and absorb cell wall components.

DIGESTION OF PLANTS BY HERBIVORES

Herbivorous mammals can be broadly divided into three types according to digestion. Type 1 herbivores have a large fermenting organ in front of the stomach, and this type includes cows and goats. Type 2 herbivores have a large intestine and cecum with a large volume in which fermentation occurs, and this type includes rabbits and horses. This group is further divided into two subtypes: a subtype that conducts coprophagia, such as rabbits (2a), and a subtype that does not conduct coprophagia, such as horses (2b). Type 3 herbivores, such as giant pandas, have a digestive tract that is not much different from that of carnivorous animals. This type of herbivore does not have a large fermenting organ. The features of each digestion type are briefly described below.

Type 1 has a large fermenting organ in front of the stomach

Cows are known to have four stomachs. The rumen (1st stomach) is a very large organ where bacteria ferment food. It produces alcohols and volatile fatty acids, such as acetic acid, propionic acid and butyric acid, which are then absorbed. Fermentative bacteria increase exponentially at this site. The reticulum (2nd stomach) is located at the base of the esophagus, near the entrance to the rumen, and is a ruminant motor organ that returns poorly chewed food to the mouth. The ruminant returns the food to the mouth where it is chewed again before being sent to the rumen. Well-degraded food passes through the reticulum and is sent to the omasum (3rd stomach). The omasum is located on the anal side of the reticulum and has a file-like mucosa that provides the final mechanical crushing of food. The first to third stomachs are thought to be derived from the esophagus. The final stomach, the abomasum (4th stomach), produces gastric acid. Here, the food is chemically degraded, and the increased bacterial cells are destroyed by gastric acid. Then, in the small intestine, both the gastric residue and the degraded bacterial cell components are digested and absorbed.

Type 2 uses the cecum and the large intestine as large fermenting organs

Type 2a herbivores conduct coprophagia: In rabbits, food that is consumed orally passes through the stomach and into the small intestine, similar to the process in humans. First, the stomach absorbs nutrients that can be digested and absorbed. Indigestible polysaccharides, mainly cell walls, are degraded and fermented by bacteria in the dilated cecum and the oral side of the large intestine. The absorbable nutrients such as short-chain fatty acids (SCFAs), mainly volatile fatty acids, are absorbed instantly. Nutrients that are difficult to absorb by the large intestine, such as vitamins synthesized by intestinal bacteria, pass through the stomach again by coprophagia and are absorbed by the small intestine.

Type 2b herbivores do not conduct coprophagia: In horses, food that is consumed orally passes through the stomach and into the small intestine, similar to the process in rabbits. First, the stomach absorbs nutrients that can be digested and absorbed. Indigestible substances are degraded and fermented by bacteria in the cecum and oral side of the dilated large intestine to absorb nutrients. However, since coprophagia is not normally conducted, the efficiency of decomposition and absorption of nutrients is considered lower than that of rabbits and other animals engaging in coprophagia. This type of gastrointestinal tract is long, but it is similar to that in humans. Since the analysis of horse intestinal flora has been sufficiently advanced, we compare horse and human intestinal bacteria in the subsequent section.

Type 3 does not have a large fermenting organ

Giant pandas are herbivores that eat bamboo as their staple food; however, their digestive tract is said to be similar to that of carnivores. The intestinal bacteria found in giant pandas have been reported to be distinct[3].

THE INTESTINAL BACTERIA OF HORSES COMPARED TO THOSE OF HUMANS

Humans do not have a large cecum like horses, although the ascending colon to transverse colon is wide, and fermentation by intestinal bacteria occurs in this area. In humans, bacteria that are ingested orally are killed by gastric acid (pH: 1.5-2.0), which is more acidic than that in horses (pH: 4.4)[4]. Thus, the number of intestinal bacteria is very small on the oral side of the small intestine. However, intestinal bacteria increase rapidly from the proximal end to the distal end of the small intestinal tract. Moreover, gut bacteria progress from aerobic bacteria to anaerobic bacteria with increasing distance in the small intestine. By the ileocecal valve, the bacterial count increases to 10^7-10^9/mL and eventually increases to approximately 10^{10}-10^{12}/mL in the colon[5]. It is estimated that this flora contains 500-1000 different species of bacteria[6], with nearly 80% belonging to the two bacterial phyla *Bacteroidetes* and *Firmicutes*[7].

Table 1 shows a modified report of the horse gut microbiota compiled by Kauter *et al*[8]. This table summarizes whether microorganisms found in the intestinal tract of horses are also found in humans. The gram-negative bacilli *Bacteroides thetaiotaomicron* and *B. ovatus*, which metabolize complex dietary polysaccharides, have been found in the human intestine and have been reported to be involved in the degradation of plant cell walls[9]. The genus *Bacteroides* has been reported to increase in abundance in the large intestines of horses that consume increased proportions of grass[10]. *Bacteroides* is also a cell wall-degrading bacterium that accounts for a large proportion of the intestinal flora in both humans and horses[7]. In addition, some bacterial species reported in humans have been identified as cell wall-degrading bacteria. Therefore, these bacteria were added to create a table. From this table, it can be seen that many species of horse bacteria are also present in the human colonic flora. In other words, the intestinal bacteria of humans can degrade plant cell walls and synthesize SCFAs, including volatile fatty acids. These SCFAs can be absorbed by the large intestine[11]. Horses can obtain energy from this system. This raises the question of how much energy humans obtain from the cell wall.

CALORIES DERIVED FROM THE CELL WALL IN HUMANS

In general, a reference for the current caloric contribution of food was determined by S ánchez-Peña *et al*[12]. This reference includes the inputs of carbohydrates 4 kcal/g, lipids 7 kcal/g, and proteins 4 kcal/g, and the input of alcohols 7 kcal/g was recently added. In recent years, it has been recommended to display these values in joules, *i.e.*, carbohydrates 17 kJ/g, lipids 37 kJ/g, proteins 17 kJ/g, and alcohols 29 kJ/g. One calorie is approximately 4.186 J, and there is a slight difference between the cal display and the J display. The standards are set by the national institutions of each country. There are differences between countries regarding items, but there are no differences in the basic amount of heat. The Food and Agriculture Organization has proposed adding dietary fiber to the calorie calculation, and 2 kcal/g and 8 kJ/g have been adopted in countries that add dietary fiber calories to the calculation[13]. Dietary fiber has fewer calories than carbohydrates because watery dietary fiber is calculated as calories. However, insoluble dietary fiber, which is the main component of plant cell walls, is not used in calorie calculations.

We further considered how much dietary fiber actually becomes calories. We examined the extent to which dietary fiber becomes calories. Dietary fiber that is fermented is generally considered to be soluble dietary fiber. However, since bacteria that degrade insoluble dietary fiber, such as cellulose, also exist in humans, as described above, insoluble dietary fiber is slightly degraded by fermentation in the intestinal tract of humans. The caloric content of cellulose was reported to be 4.16 kcal/g[14]. However, it is estimated that there will be large individual differences in the acquisition of calories based on not only whether the cellulose is raw or cooked but also the influence of cell wall strength, the intestinal flora and intestinal residence time. Elia and Cummings[15] suggested that 70% of dietary fiber is fermented. A total of

Table 1 Enterobacteria that break down fibers derived from cell walls

Family	Genus		Species	Putative effects	Horse		Human	
						Ref.		Ref.
Acidaminococcaceae	*Phascolarctobacterium*	spp.		Fiber fermenters	+	[21]	+	[22]
Bacteroidaceae	*Bacteroides*	spp.		Plant wall degradation	+	[7]	+	[7]
			ovatus	Polysaccharide decomposition; Plant wall degradation	N/A		+	[9]
			thetaiotaomicron	Complex polysaccharide decomposition	N/A		+	[9]
Clostridiaceae	*Clostridium*	spp.		Cellulolytic, fibrolytic	+	[8]	+	[23]
Eubacteriaceae	*Eubacterium*	spp.		Cellulolytic, fibrolytic	+	[8]	+	[23]
Fibrobacteraceae	*Fibrobacter*	spp.		Plant wall degradation	+	[7]	N/A	
			intestinalis	Plant wall degradation	+	[24]	N/A	
Lachnospiraceae	*Butyrivibrio*	spp.		Cellulolytic, fibrolytic	+	[8]	+	[25]
	Blautia	spp.		Fiber fermenters	+	[26]	+	[27]
Prevotellaceae	*Prevotella*	spp.		Fiber fermenters	+	[26]	+	
			copri	Fiber fermenters	N/A		+	[28]
Ruminococcaceae	*Ruminococcus*	spp.		Cellulolytic, fibrolytic bacteria	+	[8]	+	
			albus	Plant wall degradation	+	[8]	+	[29]
			bromii	Plant wall degradation	N/A		+	[30]
			champanellensis sp.nov.	Plant wall degradation	N/A		+	[31]
			flavefaciens	Plant wall degradation	+	[32]	+	[33]
			sp.nov.	Plant wall degradation	N/A		+	[34]

Based on the intestinal flora of horses compiled by Kauter *et al*[8], we selected microorganisms that decompose cell walls and summarized whether they exist in the human large intestine. Several bacterial species reported in humans as cell wall-degrading bacteria are added to the Table. N/A: Not available.

51.0% of the energy initially present is lost through feces, and 3.5% is lost through H_2 and CH_4 gaseous products. It is assumed that the remaining 45.5% is energy that can be absorbed and metabolized by human tissues[15]. Based on this calculation, the calories of dietary fiber were set to approximately 2 kcal/g and 8 kJ/g.

In the 1980s, when it was thought that cellulose could not be digested by humans, tests were conducted on humans using radioactive isotopes to examine the degradation of cellulose. ^{14}C-cellulose was given to each of 10 healthy subjects, and stool and breath samples were collected for 7 d. A wide range of variations in ^{14}C recovery were recorded, with 57% in feces, 16% in respiration as $^{14}CO_2$. The total recovery rate of ^{14}C was reported to be 73%[16]. Some of the $^{14}CO_2$ recovered by respiration was metabolized by intestinal bacteria and absorbed through the large intestinal mucosa. The remaining 27% did not recover and may have been incorporated into the body. At the time, it was suspected that the study did not use pure cellulose but used cellulose containing starch. However, it has since been proven that cellulose is degraded by gut bacteria. Therefore, this study is considered to provide valuable human data. The wide range of variations in ^{14}C recovery may be related to differences in intestinal bacteria and different lengths of stay in the gastrointestinal tract. This study showed that 27%-43% of cellulose could have been used by humans. As mentioned above, the actual cell wall is made of more than indigestible cellulose alone, and it is estimated that the actual amount utilized by humans is below this value. Therefore, it is understandable that the cell wall, which is classified as water-insoluble dietary fiber, is not added to the caloric calculation.

Ninety to ninety-five percent of the SCFAs produced in the large intestine by the fermentation of dietary fiber, including watery dietary fiber, are absorbed by the large intestine[17]. It has been reported that SCFAs absorbed in the colon contribute 6% to

10% of the total energy requirement of humans and that this contribution is probably increased in humans who consume more fiber[18,19]. Currently, the United States Food and Drug Administration (FDA) has set the recommended daily intake (RDA) of fiber at 38 g/d and 25 g/d for healthy men and women, respectively, aged 19-50 years. However, most Americans are reportedly not consuming the recommended dietary fiber intake. In other words, even if the encouraged fiber intake is met and is completely converted into energy, it amounts to approximately 150-100 kcal. Therefore, the proportion of dietary fiber in the total amount of energy in the current diet is minimal [20].

CONCLUSION

Water-insoluble dietary fiber derived from plant cell walls is considered to be indigestible dietary fiber, and it is difficult to ferment and degrade. However, many species of bacteria present in the intestines of herbivores are also found in the digestive tract of humans. Therefore, it is possible that the dietary fiber derived from plant cell walls is degraded to some extent, even in the digestive tract of humans, and used as energy. Since the amount of dietary fiber in the total food intake is minimal, the calorie intake is minimal. The main reason why it is difficult to degrade dietary fiber derived from plant cell walls is that cellulose, which is difficult to degrade, is in a firmly solidified state integrated with hemicellulose, pectin, lignin, suberin, and other components. If cellulose can be separated from these other components and degraded, it is possible that plant cell walls can contribute more calories in humans than when cellulose is combined with the other cell wall components. The cell wall contains a large amount of potential energy. Thus, if the amount of energy utilized from the cell wall by cell wall-degrading bacteria can be increased, the food situation in food-deficient areas can be expected to improve. Currently, bioethanol is being developed, and its dietary use in the degradation of cell walls is anticipated.

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