



Cellulase-producing Microorganisms from Diverse Ecosystem: A Review

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Cellulose is the most abundant organic matter present on the planet. It is made up of glucose molecules which is the ultimate energy currency. Still, cellulose is utilized by most the animals as energy source as they lack necessary enzymes for degradation of the molecule. The animals who are able to utilize cellulose based materials as source of energy are able to do so due to cellulase producing gut microflora. Cellulases are enzymes which are used by certain organisms to breakdown the cellulose. Very small number of organisms are able to produce different types of cellulases which can break the bonds present in cellulose molecules. Only few bacteria, fungi and protozoa have necessary genes for cellulase. It has been found that certain herbivorous insects are also able to synthesize their own cellulase but again this property is very limited in few insect types. The microorganisms who are able to synthesize cellulase are present in soil and water along with certain mammalian and insect guts. In soil and water such microorganisms decompose the dead plant matter containing cellulose and help in maintaining the carbon cycle along with getting energy from the molecule. Apart from ecological activity the cellulases are utilized for various industrial

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purposes. In the current review we have discussed different types of microorganisms which are able to produce cellulases. The source of such microorganisms are also discussed briefly to place them in the right context.

Keywords: Cellulase; bacteria; fungi; insects; cellulose; animals.

1. INTRODUCTION

Cellulose is one of the world's most prevalent polysaccharide that is widely found in plants and makes up 40–50% of their cell walls. It is the most prevalent structural component of these materials. It keeps the plant upright and rigid. In addition, oomycetes and algae also contain it (Gupta et al. 2019). The composition of cellulose is hydrogen, oxygen and carbon. The β -D glucopyranose monomers are joined by 1,4 glycosidic bonds to form a linear polymer chain. All of the hydroxyl groups (O–H) are positioned on the equatorial locations of the folded glucan ring, whereas the methine groups (C–H) are positioned on the axial positions. Naturally it occurs as I α and I β , two crystalline forms (Makarem et al. 2019).

Animals need cellulase enzyme, which facilitates the breakdown of cellulose, so they can convert it into glucose and use it as nutrition. However, they lack the ability to generate cellulase; only bacteria, fungi, and protozoa can break down cellulose and produce glucose, and some specific insect species can do it as well. Many Herbivorous and omnivorous insects like some species of cockroach, grasshopper, termites, mammals have symbiotic microorganism in their gut that aid in the breakdown of cellulose, and some insect species such as silverfish, cockroach, termites are capable of producing their own cellulase in their gut or salivary gland (Wada-Katsumata and Schal 2021).

Insects' guts are home to a wide variety of microorganisms, including symbiotic bacteria and fungus, which help to purify the host's gut, supply nutrients, boost immunity, shield insects from parasites and infections. During their feeding process, herbivorous insects such as termites, beetles, grasshoppers, butterflies, and others ingest cellulose. Their intestinal bacteria that produce cellulase break down lignocellulose and generate glucose, which serves as a significant source of energy for these insects. Protozoa, fungi, and bacteria are all capable to manufacture the enzyme cellulase, even though bacterial cellulase has been utilized extensively because of its steady state of reaction as well as quick incubation period.

(Li et al. 2023). Cellulose-degrading bacteria are found in mammals such as humans, rabbits, dears, sheep, goats, cows, and others. Protozoa also capable to digest cellulose are found in rumen including cows, sheep, and goats. The ecosystems of both water and soil are habitat to cellulose degrading bacteria and fungi. Compared to protozoa or fungi, the growing procedure for cellulose degrading bacteria is far simpler and less expensive. Because of this, there is a great need for these microorganisms in the industrial sector. These microorganisms aid in composting, nutrient cycling, organic matter breakdown, biodegradation, waste management, and bioremediation. Cellulose-degrading bacteria are a great gift for the textile, pulp and paper, wine, and biofuel industries (Wang et al. 2024). This review examines the sources of cellulase enzymes, focusing on the environments where they are typically found. Understanding these factors will provide valuable insights into the production and applications of cellulase enzymes.

2. SOURCES OF CELLULASE

Cellulase, also referred to as 4- β -D-glucan 4-glucanohydrolase, is necessary for the breakdown of cellulose into glucose so that energy can be produced. This enzyme is classified into three main types: β -glucosidase (EC 3.2.1.21), 1,4- β -endoglucanase (EC 3.2.1.4), and 1,4- β -exoglucanase (EC 3.2.1.91). All three of these enzymes cooperate with one another to hydrolyse cellulose in an orderly way. Cellulase enzyme is found in two sources: insects and microorganisms like bacteria, fungus, and protozoa. (Fig. 1).

3. MICROBIAL SOURCES OF CELLULASE

Like the majority of other enzymes, cellulase enzymes have soluble substrates that transport into their active sites. In order to perform cleavage, the cellulase enzyme must also diffuse to its insoluble ingredient as well as draw a chain of polymers within the site of activity. Certain aerobic microbes discharge a collection of distinct cellulases using the free cellulase

system, that collaborate in concert to break down cellulose. The specific activity of suitable combinations can be increased as much as fifteen times through cellulase harmony as opposed to solo cellulases (Fischer et al. 2013).

Cellulosomes are huge multienzyme complexes that are used by certain anaerobic microorganisms to break down cellulose. The cellulosome scaffold provides the carbohydrate-binding domain, which is present in only a small number of the enzymes inside insect cellulases. It facilitates the binding of the substrate's whole complex. A tiny percentage of anaerobic cellulolytic thermophilic bacteria, including *Caldicellulosiruptor* species, do, nevertheless, release free cellulases that have features to connect carbohydrates. In contrast to the majority of other cellulolytic bacteria, it may convert plant material with no any prior preparation (Fischer et al. 2013).

The cellulase enzyme usually exists in fungi, protozoa, and bacteria. (Fig. 1)

Fungi: The two most crucial variables for the synthesis of the cellulase enzyme are temperature and pH. The fungus requires a pH of 3.0 to 7.0 and a temperature of 40° to 50° to produce cellulase. Numerous fungal species, including *Aspergillus*, *Trichoderma*, *Penicillium*, *Humicola*, *Acremonium*, *Rhizopus*, *Beauveria*, and *Bassiana*, may produce an enzyme that breaks down cellulose, however *Aspergillus niger* and *Trichoderma reesei* can produce far more cellulase (Amer and Bibi 2018).

Protozoa: Cellulase, which helps them flourish by turning cellulose into glucose, can be produced by flagellate protozoans like *Pelamyxa*

and *Trichonympha*, which are present in termite eaten wood, and rumen protozoans like *Epidinium ecauda-tum*, which are found in animals' rumen (Ashraf et al. 2019).

Bacteria: A number of bacteria have the capacity to generate cellulase enzyme in order to adequately satisfy their nutritional requirements. Bacteria are divided into three distinct groups based on their respiration type: aerobic, anaerobic and facultative anaerobic. Aerobic, anaerobic and facultative anaerobic bacteria both can be able to degrade cellulose which they collect from plant cell wall (Thapa et al. 2020). The cellulose-degrading bacteria and their categorization are discussed in the Table (Table 1).

4. INSECTS SOURCE OF CELLULASE

The most widespread group of species on the world is insects who occupy nearly every ecological niche. In order to survive in a variety of sometimes harsh environments, insects have developed a wide range of biological and chemical systems. Enzymes that allow the insects to consume a variety of food sources are essential parts of these systems. Either the insects themselves, which is known as homologous, or symbiotic organisms found in the insects' bodies or nests create the enzymes (Abid et al. 2024). One of these enzymes known as cellulase, breaks down cellulose in glucose. Certain insect species naturally have these enzymes that aid in the breakdown of cellulose. Table 2 provides a quick overview of insects that are capable of producing their own cellulase enzyme. (Table 2) (Fig. 1).

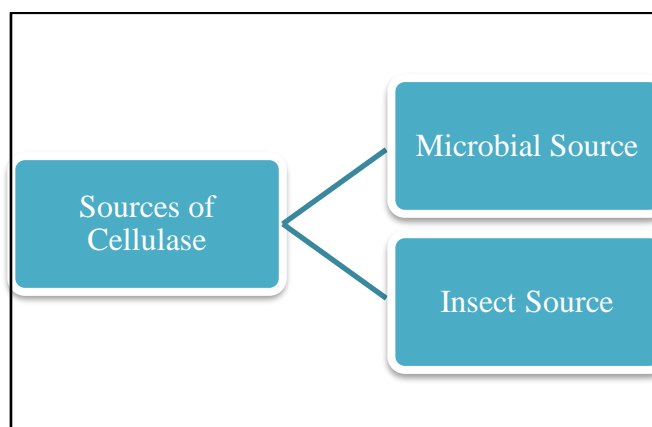
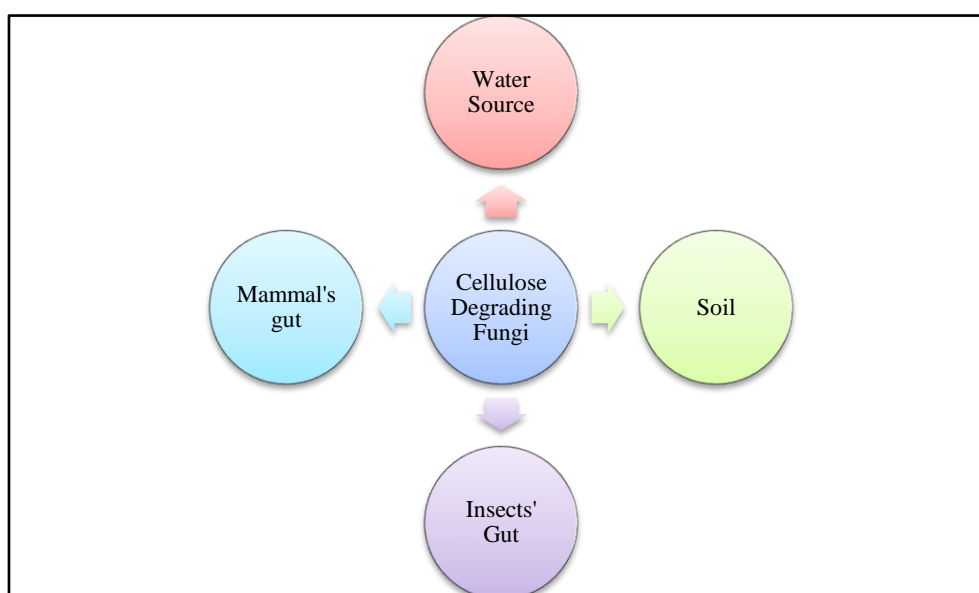


Fig. 1. Sources of cellulose degrading bacteria

Table 1. List of Cellulose degrading bacteria and their Scientific Classification

Bacterial Species	Genus	Respiration Type	Stain Type	References
<i>Bacillus nakamurai</i>	Bacillus	Aerobic	Gram Positive	(Shaikh et al. 2023)
<i>Bacillus subtilis</i>	Bacillus	Facultative aerobic	Gram Positive	(Deng and Wang 2022)
<i>Streptomyces drozdowiczii</i>	Streptomyces	Aerobic	Gram Positive	(Celaya-Herrera et al. 2021)
<i>Streptomyces reticuli</i>	Streptomyces	Aerobic	Gram Positive	(Yang et al. 2022)
<i>Clostridium thermocellum</i>	Clostridium	Anaerobic	Gram positive	(Nhim et al. 2022)
<i>Cellulomonas flavigena</i>	Cellulomonas	Facultative Anaerobic	Gram Positive	(Li et al. 2021)
<i>Thermobifida fusca</i>	Termobifida	Aerobic	Gram Positive	(Wu et al. 2022)
<i>Clostridium cellulolyticum</i>	Clostridium	Anaerobic	Gram Positive	(Tao et al. 2020)
<i>Caldicellulosiruptor bescii</i>	Caldicellulosiruptor	Anaerobic	Gram Positive	(Straub et al. 2020)
<i>Fibrobacter succinogenes</i>	Fibrobacter	Anaerobics	Gram Negative	(Fakih et al. 2023)
<i>Ruminococcus albus</i>	Ruminococcus	Anaerobic	Gram Positive	(Weimer 2022)


Fig. 2. Sources of Cellulose degrading Bacteria

5. DIFFERENT ENVIRONMENT OF CELLULOSE DEGRADING BACTERIA

Water source: There are several kinds of bacteria in water, both harmful and non-harmful. Cellulose-degrading bacteria that aid in the degradation of aquatic weeds that polluting water along with improving the water's quality. The

cellulose-degrading bacterium *Bacillus* sp. W12 is found in water sources as well as may help to enhance the level of quality (Dat et al. 2019). (Fig. 2)

Soil: Numerous bacterial species can be found in soil, which is a major microbial hub on Earth. It is a significant source of carbon sinking on land.

A sizable bacterial component of the soil aids in the breakdown of dead plant matter, which is mostly composed of different plant cell wall polymers like cellulose, hemicellulose, and lignin (Datta 2024). Numerous soil bacteria, including *Serratia marscens*, *Bacillus subtilis*, *E. coli*, and *Pseudomonas fluorescens*, are capable of producing the cellulase enzyme, which completely converts cellulose to glucose (Kukreti et al. 2024). Bhagat and Kokitkar (2021), reported the common soil bacterium *Bacillus* species have the greatest capacity to degrade cellulose. Soil-derived microorganisms that break down cellulose have been the subject of numerous published reports. In recent years, several bacteria that have the ability to break down cellulose have been isolated from soil, including *Bacillus sphaericus* BS-5 (Xu et al. 2017) and *B. subtilis* K1 (He et al. 2023). (Fig. 2)

Insects'gut: The relationship between insects and intestinal microbes is quite complicated. In addition to being beneficial, insects' gut microbes assist in the digestion process. In order to aid in the digestion of the plant materials they eat, herbivorous and omnivorous insects form symbiotic relationships alongside bacteria that break down cellulose (Taggar 2015). These insects include, among others, Cotton Bollworm (Madhusudhan et al. 2021), *Glenea cantor* (Su et al. 2024), *Bombyx mori* (Prem Anand et al. 2010), mole crickets (Patel et al. 2024), lower termites (Tsegaye et al. 2019), cockroaches (Cruden and Markovetz 1979), and grasshoppers (Munir et al. 2024). A brief discussion of insects that can generate the cellulase enzyme with the support of symbiotic gut bacteria is provided in Table 2. (Table 2) (Fig. 2).

Mammal's' gut: Plant cell walls are composed of pectin, cellulose, and hemicellulose. Mammals that are herbivorous or omnivorous ingest 10% to 28% of the cellulose found in the dry matter of raw plant materials, besides as much as seventeen percent of the dry matter of human diets contains cellulose. Cellulose can be either crystalline or amorphous and is made up of connected d-glucose units. Because of its arrangement, this polysaccharide is complicated. Mammals' upper guts neither digest nor absorb it; instead, it is broken down by a symbiotic relationship between cellulolytic microbes and their host. As a result, bacteria that break down cellulose are essential for producing energy from food as well as improving the health of the host (Froidurot and Julliand 2022). Talk about the mammals that have cellulose-breaking bacteria

and their favourite foods in beneath the table. (Table 3) (Fig. 2).

6. DIFFERENT ENVIRONMENT OF CELLULOSE DEGRADING FUNGI

Dead wood or litter: The non-living plant material known as dead wood or litter is composed of cellulose, hemicellulose, and lignin. Without any kind of microorganism, the decomposition of dead wood is a challenging endeavour. Certain forms of fungi aid in the breakdown of cellulose. Some of the most powerful cellulose degraders are basidiomycetous fungus, which frequently proliferate in the environment (Baldrian and Valášková 2008). (Fig. 3)

Soil: A type of microorganisms known as fungi are found throughout the environment, but soil is the ideal habitat for them. They are nocturnal in the natural world yet they also generate a wide range of enzymes that are hydrolytic. There are several types of fungus that can be found in soil, including Ascomycetes, Basidiomycetes, Deuteromycetes, Trichocladium, Chaetomium, Dactylaria, Arthrotrichum, Sarocladium strictum, Cladosporium ramotenellum, Pleosporales sp., Peniophora incarnate, Aspergillus foetidus, Dothideomycetes, and Penicillium griseofulvum (Viikari et al. 2009). (Fig. 3).

Water: Microbes that break down cellulose are among the many microbial consortiums found in water, and they contribute to the filtration procedure. A kind of actinomycetes known as micromonospora often occurs in great quantities in soil, yet they are highly suited to water and break down cellulose (de Menezes et al. 2008). (Fig. 3).

Insects' gut: A symbiotic relationship between insects and fungi aids in the digestion of cellulose. The cellulolytic mechanisms of fungi and bacteria are not the same. Due to the higher activity of fungal cellulases compared to bacterial cellulases, the fungal cellulolytic process is typically simpler in downstream method. According to Takasuka et al. (2013), a white rot fungus designated as *Amylostereum areolatum* has been identified from the *Sirex* insects. According to Carbonero-Pacheco et al. (2023), *Phenicillium*, *Rhizopus*, *Trichoderma*, *Aspergillus*, *Fusarium*, *Mucor*, *Neurospora*, *Alternaria*, and *Acremonium* were isolated from termite. (Fig. 3)

Table 2. List of insects where present of cellulose degrading bacteria or own cellulase enzyme

Name of Insects	Phylum	Order	Cellulose degrading bacteria/ Own cellulase enzyme	Food Class	References
Cockroach	Arthropoda	Blattodea	<i>Bacteroides sp.</i> <i>Clostridium sp.</i> yellow strain of <i>Chryseobacterium sp.</i> and also produce own cellulase enzyme	Omnivorous	(Carvalho et al. 2022)
Cotton bollworm or <i>Helicoverpa armigera</i> .	Arthropoda	Lepidoptera	<i>Klebsiella sp.</i>	Herbivorous	(Dar et al. 2021)
<i>Sitophilus oryzae</i> or Lesser grain weevil or rice weevil	Arthropoda	Coleoptera	<i>Staphylococcus Sp.</i> <i>Bacillus Sp.</i>	Herbivorous	(Nandy et al. 2021)
Grasshopper	Arthropoda	Orthoptera	<i>Enterobacteriaceae, Bacteroides, Staphylococcus, Streptococcus, and Bacillus.</i>	Herbivorous	(Gur Ozdal and Algur 2022)
Lower termite	Arthropoda	Blattodea	<i>Dipolcocci sp.</i> , <i>Diplobacilli sp.</i> , <i>Streptobacilli sp.</i> and <i>Staphylococci sp.</i>	Herbivorous	(Xie et al. 2021)
Higher termite	Arthropoda	Blattodea	Produce own cellulase enzyme	Herbivorous	(Zhou et al. 2019)
Silverfish	Arthropoda	Zygentoma	Produce own cellulase enzyme	Herbivorous	(Pothula et al. 2020)
Caterpillar,	Arthropoda	Lepidoptera	Not Identified	Herbivorous	(Nandy et al. 2021)
Mole crickets	Arthropoda	Orthoptera	<i>Acinetobacter junii</i>	Herbivorous	(Nandy et al. 2021)
<i>Bombyx mori</i>	Arthropoda	Lepidoptera	<i>Solibacillus silvestris</i> , <i>Bacillus aryabhattai</i> , <i>Lysinibacillus sp.</i> , <i>Bacillus sp.</i> , <i>Bacillus thuringiensis</i> , <i>Paenibacillus sp.</i> , <i>Serratia marcescens</i> , <i>Klebsiella pneumonia</i> and <i>Enterobacter hormaechei</i>	Herbivorous	(Pandiarajan et al. 2020)

Table 3. A list of mammals, alongside the bacteria that break down cellulose and their preferred foods

Mammal's Name	Scientific Name	Bacteria	Food Preference	References
Human	Homo sapiens	<i>Ruminococcus primaciens</i> , <i>Ruminococcus champanellensis</i> sp. <i>Ruminococcus hominiciens</i> , <i>Ruminococcus ruminiciens</i> , <i>Bacteroides cellulosilyticus</i> and <i>Enterococcus faecalis</i>	Fruit, vegetables, flowers, meat etc.	(Moraïs et al. 2024, Chassard et al. 2012, Chassard et al. 2010)
Rabbit	Oryctolagus cuniculus	<i>Clostridium sartagoforme</i>	Fresh vegetables	(Gong et al. 2021)
Elephant	Loxodonta	<i>Fibrobacter succinogenes</i>	Plant materials	(Froidurot and Julliand 2022).
Cow	Bos Taurus	<i>Ruminococcus albus</i> , <i>Ruminococcus flavefaciens</i> , and <i>Fibrobacter succinogenes</i> .	Plant materials	(Russell et al. 2009)
Horse	Equus caballus	<i>Bacteroides</i> , <i>Bacillus cellulose dissolvens</i> , <i>Gram-negative coccobacillus</i> , <i>Gram-negative curved rod</i>	Grass and hay	(Froidurot and Julliand 2022).
Donkey	Equus asinus	<i>R. flavefaciens</i>	Grass, hay, grains, Legumes, fruit and vegetables.	(Froidurot and Julliand 2022).
Guinea pig	Cavia porcellus	<i>Ruminococcus spp.</i>	Hay, Leafy greens or weeds, vegetables and fruits.	(Froidurot and Julliand 2022).
Goat	Capra aegagrus hircus	<i>Fibrobacter succinogenes</i> , <i>Ruminococcus flavefaciens</i> , <i>Ruminococcus albus</i> , and <i>Butyrivibrio fibrisolvens</i>	Fresh clean grass, leaves, vegetables	(Turaeva et al. 2023)
Sheep	Ovis aries	<i>Enterobacter cloacae subsp. Dissolvens</i> , <i>Bacillus sp.</i>	grass, leaves, and leafy greens	(Guder and Krishna (2019).
Koala	Phascolarctos cinereus	<i>Bacillus sp. and Pseudomonas sp.</i>	Eucalyptus leaves	(Singh et al. 2015)
Sika Deer	Cervus nippon hortulorum	<i>Prevotella spp.</i>	oak leaves	(Lan et al. 2021, Li et al. 2015)

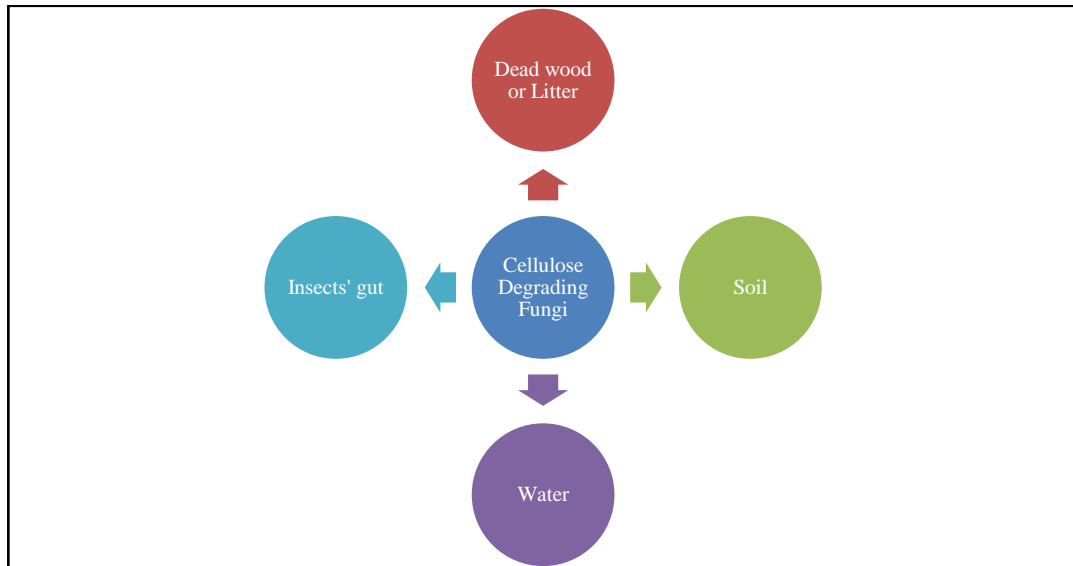


Fig. 3. Sources of Cellulose Degrading Fungi

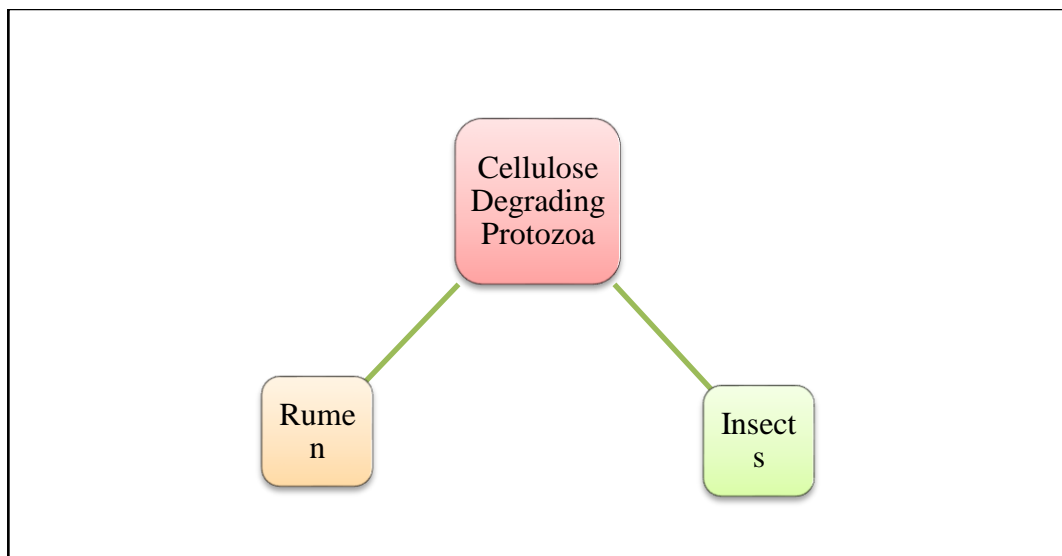


Fig. 4. Sources of Cellulose Degrading Protozoa

7. DIFFERENT LOCATION OF CELLULOSE DEGRADING PROTOZOA

Rumen: Protozoa belong to the kingdom Protista and are single-celled creatures. It is found in a variety of circumstances, such as soil, water, insect body, and human body (Meshjel 2024). Although they need a moist environment to survive but some kind of can do so by developing resting cysts. A certain kind of protozoa can break down the cellulose. Protozoa of this sort are located in the rumen body and play a significant role in the breakdown of plant resources. One anaerobic microbe that is crucial

to the digestion of cellulose in the rumen body is *Epidinium ecauda-tum* (Amer et al.2018) (Fig. 4).

Insects: The gut of insects contains a variety of protozoa that are helpful in the digestive process of food, in particular the harder-to-digest elements of food. Some of those have the capacity to break down cellulose. According to Tokuda et al. (1997), many protozoa are found in an expanded portion of the hindgut of wood-eating cockroaches and lower termites. Tokuda and Watanabe (2007) states that the flagellate protist is a symbiotic protozoa that breaks down

cellulose. This protozoa is found in termites and wood-eating roaches both. (Fig. 4)

8. CONCLUSION

Cellulase is an important enzyme but its production by organisms is very limited. Even though plants produce cellulose in huge quantity it is not utilized by all animals as source of energy because of lack of ability to produce cellulase. Very small number of microorganisms are able to produce cellulase and utilize cellulose as energy source. Mostly herbivores harbour cellulase producing microorganisms in their guts and some omnivores like humans and cockroaches have them too. No information was available in literature search about the gut microflora of other primates therefore it would not be prudent to say that they don't have any still primates including humans do not naturally utilize cellulose as energy source. Among the microorganisms who are capable of producing cellulase are bacteria, fungi and protozoa. They are decomposers who degrade the dead organic matter and help continue the carbon cycle in the ecosystem. Certain insects too have the ability to produce their own cellulases even when they harbour cellulase producing microflora in their guts.

In this review we have shown that there are enough microorganisms which are able to produce cellulases even though their actual number in larger ecosystem is less. These organisms provide a service to the ecosystem as they not only breakdown the most abundant biomolecule on the planet but also help in continuing the carbon cycle. The activity of cellulase also helps provide glucose to the organisms producing the enzyme as well those who harbour them. These microorganisms are present in almost all kind of ecosystems from soil, water, on surface of plants and their dead parts to guts of insects and higher mammals.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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