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Nitrogen fixation in the gastrointestinal tract of rodents

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ABSTRACT

This review paper presents a comprehensive overview of the presence of nitrogen-fixing activity in various parts of the digestive tract and intestinal content in the red-backed vole and the common vole. Research has shown that nitrogen fixation, the process of converting atmospheric nitrogen into forms available for biological use, does not occur uniformly across all segments of the digestive system. The highest level of nitrogen-fixing activity is observed in the wall of the large intestine, indicating the importance of this part of the gut as a site of intense microbial activity. In contrast, the lowest level of activity is recorded in the wall of the forestomach, likely due to unfavorable conditions for the development of nitrogen-fixing microorganisms in this part of the system. Furthermore, nitrogen-fixing activity in the contents of all intestinal segments in voles is significantly higher compared to control groups, confirming the presence and activity of a specific microbial community. These findings suggest that gut microorganisms in rodents play an important role in nitrogen supplementation, which may be crucial for the nutritional strategy of these animals, especially given the low nitrogen content of plant-based food sources. This paper contributes to a better understanding of microbiological and biological processes in the digestive tract of rodents and opens the way for further research in the field of their ecology and nutritional adaptation.

Keywords: *nitrogen fixation, vole, wall, microorganisms, content, intestine.*

INTORDUCTION

One of the traditional challenges in soil science is understanding the role of animals in pedogenesis and the biogenic cycling of elements, among which nitrogen holds a central position due to its importance in plant and animal metabolic processes.

Although it is well known that numerous animal species participate in the transformation of organic and mineral components of the soil, data on the influence of the most widespread and numerous among them, rodents, on microbiological processes related to nitrogen remain fragmented (Jemcev and Đukić, 2000; Đukić et al., 2007).

Rodents are an ecologically significant group of mammals, characterized by intensive space utilization and the ability to inhabit relatively small territories over the long term. Their role in soil dynamics and biological activity in the soil, including their potential contribution to the nitrogen cycle, has not been sufficiently investigated to date.

One of the least understood aspects of the diet of herbivorous mammals, especially small phytophagous species such as voles, is how they obtain adequate amounts of nitrogen through their diet. A plant-based diet composed primarily of grass is rich in cellulose but poor in protein and nitrogen, presenting a challenge for meeting nitrogen requirements in these organisms (Bizov, 2001). The fermentation of cellulose in the digestive tract requires the presence of microsymbionts, bacteria and protozoa, that enable the breakdown of complex carbohydrates. In larger herbivores, such as ruminants, this process occurs in specialized fermentation chambers like the rumen, whereas in smaller mammals, the compensatory mechanisms are not fully understood (Naumova, 1999).

In this context, one possible solution to this nutritional challenge may lie in the presence and activity of nitrogen-fixing microorganisms in the digestive tract of rodents. Nitrogen fixation, as the process of converting atmospheric nitrogen (N_2) into forms usable by organisms, represents a potential additional source of nitrogen that could significantly contribute to the host's nutrition. Although this phenomenon has been extensively studied in other organisms and in symbiosis with plants, systematic data on its presence in the intestinal tract of rodents has only recently begun to emerge.

The aim of this review paper is to present the existing data on nitrogen-fixing activity in various parts of the gastrointestinal tract and intestinal contents of two vole species—the red-backed vole and the common vole. Particular emphasis is placed on the localization and intensity of nitrogen fixation in specific segments of the digestive system, as well as on the role of microorganisms in this process. The data presented open up new possibilities for a deeper understanding of the microbiological function of the rodent gut flora in the context of the nitrogen cycle and their adaptation to a nitrogen-poor diet.

NITROGEN-FIXING MICROORGANISMS IN THE DIGESTIVE TRACT OF RODENTS

The first investigation into the contribution of nitrogen-fixing microorganisms to the nitrogen nutrition of rodents was conducted using the gut contents of red-backed voles (*Clethrionomys rutilus*) (Vecherskii et al., 2014).

Control animals were fed moist legume seeds, peas and beans, which contain high amounts (22.6–23.5%) of digestible crude protein. The experimental group was given a protein-nitrogen-poor diet consisting of dandelion leaves, raw, and dried apples.

Nitrogen fixation was examined in the following parts of the gastrointestinal tract: the forestomach and the cecum (the primary sites of microsymbiont-cellulolytic activity), as well as in the large intestine, which functions to separate the bacterial mass and return it to the cecum. In addition, soft feces, consumed by voles in the process of coprophagy, were also analyzed.

Varying levels (intensity) of nitrogen fixation were detected in all samples of both gastrointestinal contents and gut wall tissues of the red-backed vole (Table 1).

A relatively low level of nitrogen fixation was observed in all samples from the control animals, which received sufficient amounts of protein nitrogen in their diet. In contrast, the nitrogen-fixing activity was significantly higher in the experimental voles, which were fed a diet low in protein nitrogen.

The highest level of nitrogen fixation was found in the large intestine of animals from the experimental group – nitrogen-fixing activity was approximately four times greater than in the voles from the control group. The lowest level of nitrogen fixation was recorded in the forestomach of the control group voles. Although nitrogen fixation in the forestomach of the experimental animals was more than ten times higher (in the gut walls), this segment of the gastrointestinal tract is still not as well adapted for the activity of nitrogen-fixing bacteria as the cecum and large intestine.

Table 1. Nitrogen-fixing activity in different parts of the gastrointestinal tract of the red vole Clethrionomys rutilus, $nMC_2H_4/g \cdot h$ (Bizov, 2001)

Vole group	**Fore-gut**		**Cecum**		**Large intestine (or colon)**		**Soft feces**
	Content	**Walls**	**Content**	**Walls**	**Content**	**Walls**	
Control	0.13	0.11	2.40	5.31	6.73	1.00	0.36
Experiment	0.21	1.80	4.83	2.79	24.39	4.65	1.93

Nitrogen-fixing activity was also higher in the cecal contents and soft feces of the experimental group voles compared to those of the control group.

The analyzed data indicate that the symbiotic communities in the gastrointestinal tract of the red-backed vole include bacterial populations capable of intensive nitrogen fixation.

Similar results were obtained for other rodent groups. In particular, the nitrogen-fixing activity in the digestive tract of the common vole (*Microtus arvalis*) – which is widespread in many ecosystems and exploits resources of relatively limited territories over long periods – has been studied (Gallon et al., 2000). A high level of nitrogen fixation was characteristic for most parts of the digestive tract, with the maximum activity detected in the contents of the cecum and large intestine (Table 2).

Table 2. Nitrogen fixation in the digestive tract of the common vole (*Microtus arvalis*), nanomol $C_2H_4/g \cdot h$ (Bizov, 2001)

Sample	**Nitrogen fixation**
Foregut	0.21 ± 0.08
Large intestine (contents)	3.31 ± 0.28
Large intestine (wall)	5.48 ± 0.35
Cecum (contents)	3.79 ± 0.39
Cecum (wall)	7.17 ± 0.55

Indeed, the contents of these intestinal segments constitute the main part of the animals' excrements, through which they exert a significant influence on the nitrogen balance in the soil at their habitats. Furthermore, the high level of nitrogen fixation in the vole's gut indirectly indicates its important role in the nitrogen nutrition of these rodents.

The global role of microbial nitrogen fixation was not immediately understood – for a long time, it was not considered when calculating nitrogen balances in the biosphere. The main reason was the lack of direct assessments of the activity and scale of the process in natural environments, as well as prevailing assumptions about the limited ability of microorganisms to fix nitrogen (Zavalin, 2005).

The widely used Kjeldahl method for nitrogen determination is poorly applicable to studying nitrogen fixation because it requires long incubation periods (up to several days) of samples in a closed environment. Previously, this method was used to examine the increase of nitrogen concentration in nitrogen-free media during microorganism cultivation, which often led to incorrect results. In this way, the ability of higher animals (chicken embryos, quails, etc.) to mobilize atmospheric nitrogen was "confirmed," which was later disproved.

The incorporation of nitrogen isotopes (stable ^{15}N and radioactive ^{13}N) into analytical practice did not simplify the task due to the specific characteristics of these isotopes.

Incorporation of the isotope marker $^{15}N_2$ into the cells of diazotrophic bacteria in an analytically necessary amount requires incubation in a closed environment from several hours up to one day, which makes practical investigation of nitrogen fixation in natural environments or natural samples difficult (Newton, 2002).

The radioactive isotope ^{13}N has a very short half-life (10.8 minutes), which is the greatest obstacle to its practical use.

The acetylene reduction assay (ARA), developed at the end of the 1970s, was the first method to enable measurement under conditions similar to natural environments — in soil, water, and sludge samples, in live animals, etc., thanks to its specific features. Among these, especially notable are its high sensitivity (10^{-9} M) and relative simplicity, which allows measurements to be performed with short incubation times, on large numbers of samples, with high reproducibility, and to obtain reliable results (Tikhonovich, 2002).

However, the acetylene method also has numerous limitations, the main one being that acetylene and molecular nitrogen molecules differ significantly in many physico-chemical properties. Additionally, as has been established, this method is practically inapplicable for determining the activity of alternative nitrogenases.

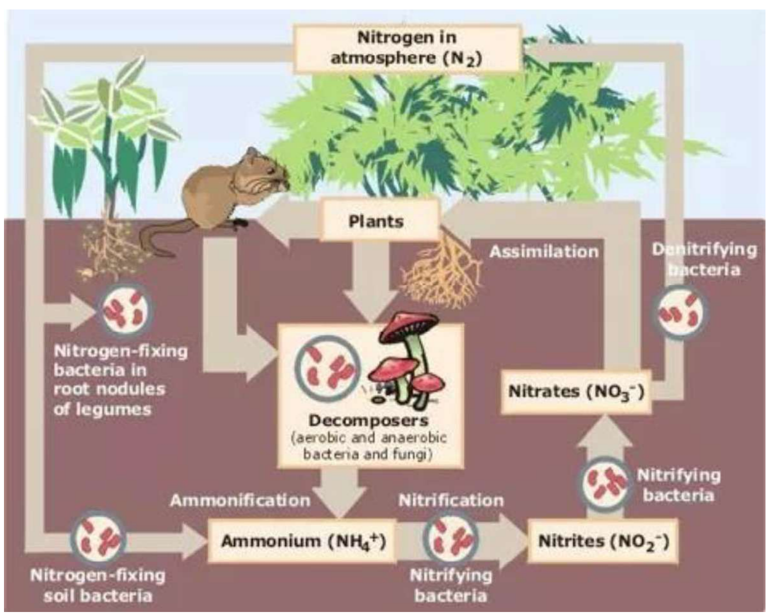

Figure 1: Nitrogen fixation (Helmenstine, 2024).

Despite these limitations, it was precisely the acetylene reduction assay that enabled the acquisition of a large amount of information about the specific characteristics of nitrogen fixation across a wide variety of ecosystems and under diverse combinations of conditions. This not only led to a rapid quantitative increase in knowledge but also to its qualitative evaluation.

The ability to fix nitrogen has been identified in the broadest range of prokaryotes, including both archaea and bacteria, which fundamentally changed the understanding of the role and place of this process in the living world. Alongside the reevaluation of the role of nitrogen fixation in the biosphere, approaches to its practical application have significantly evolved (Graham and Vance, 2003).

New and non-traditional methods of regulating nitrogen fixation are increasingly being developed – such as inoculation with mixed cultures, paranodulation, and the use of bacteria that stimulate plant growth, among others. Moreover, clarifying the close interaction between microbial nitrogen fixation and photosynthesis in plants has provided new explanations for well-known effects in crop production and agrochemistry, such as high yields based on phosphorus-potassium fertilizers and the phenomenon of "extra nitrogen" (Šabaev et al., 1985).

Finally, it became possible for the first time to assess the scale of nitrogen fixation in natural environments, revealing the leading role of terrestrial ecosystems not only in the volume of atmospheric nitrogen mobilization but also in their role in the nitrogen balance of the biosphere (Anderson, 1995).

Soil, as the site of maximum concentration of diazotrophic bacteria, serves as the main biogeochemical reactor supplying the biosphere with accessible nitrogen compounds.

Nitrogen-Fixing Microorganisms in the Digestive Tract of Rodents

The digestive tract of rodents represents a complex and dynamic ecosystem where diverse microbial communities play a key role in food digestion and nutrient metabolism. Among these, nitrogen-fixing bacteria occupy a special position due to their ability to fix atmospheric nitrogen, thereby contributing to increased nitrogen availability for the host organism.

Studies have shown that nitrogen fixation activity varies between different parts of the digestive tract, as well as between the intestinal contents and the walls of intestinal segments. For example, in voles (*Microtus* spp.), the most intense nitrogen-fixing activity is observed in the wall of the large intestine, which may be associated with the presence of specific microbial populations adapted to the conditions of this segment, such as anaerobic bacterial strains capable of nitrogen fixation (Berner and Brock, 2021).

In contrast, nitrogen-fixing activity in the forestomach wall is significantly lower, which may be due to specific physiological and chemical conditions that are unfavorable for the development of diazotrophic communities. The intestinal contents of all parts of the digestive tract also show the presence of nitrogen-fixing microorganisms, and their activity is significantly increased compared to control groups.

These results suggest that rodents, through the establishment and maintenance of microbiological populations of nitrogen-fixing bacteria in their guts, can partially compensate for nitrogen deficiency in their herbivorous diet. This enables better nutritional efficiency and adaptation to ecological conditions where nitrogen is a limiting nutrient.

Further research in this field is necessary to more precisely identify the bacterial species involved in this process, as well as to clarify the mechanism of interaction between the host and its microbiota in the context of nitrogen fixation (Berner and Brock, 2021).

METHODS FOR INVESTIGATING NITROGEN FIXATION IN THE DIGESTIVE TRACT OF RODENTS

This chapter provides a comprehensive overview of the techniques and methodologies employed in studying nitrogen fixation within the digestive tracts of rodents. Understanding these methods is essential for interpreting the current knowledge and for guiding future research in this field.

Classical Biochemical Methods

One of the foundational approaches to measuring nitrogen fixation is the acetylene reduction assay (ARA). This method relies on the ability of nitrogenase enzymes to reduce acetylene (C_2H_2) to ethylene (C_2H_4), which can be quantitatively measured using gas chromatography. The ARA test is highly sensitive, allowing detection of nitrogenase activity in different sections of the gastrointestinal tract, such as the contents and tissue walls of the stomach, cecum, and colon. However, while widely used, ARA has limitations, including potential differences in enzyme activity under assay conditions compared to natural environments.

Microbiological Techniques

Isolation and cultivation of diazotrophic bacteria from rodent gut samples are crucial for identifying specific microbial species involved in nitrogen fixation. These techniques include selective enrichment cultures under microaerophilic or anaerobic conditions, followed by phenotypic characterization and biochemical testing. Cultured isolates can be further examined for nitrogenase activity in vitro, helping to pinpoint active nitrogen-fixing strains.

Molecular Methods

Advances in molecular biology have greatly enhanced the study of nitrogen-fixing microorganisms. Polymerase chain reaction (PCR) amplification of the nifH gene, which encodes a key subunit of nitrogenase, allows for the detection and identification of diazotrophs directly from gut samples without the need for cultivation. Sequencing of nifH genes provides phylogenetic insights and helps in understanding the diversity and evolutionary relationships of nitrogen-fixing bacteria in the rodent gut. Additionally, quantitative PCR (qPCR) can estimate the abundance of nifH gene copies, serving as a proxy for the population size of diazotrophs (Smith and Osborn, 2009).

Quantification and Localization Techniques:

To understand the spatial distribution and intensity of nitrogen fixation within the digestive tract, researchers combine biochemical assays, molecular detection, and microscopy. Fluorescent in situ hybridization (FISH) targeting nifH transcripts enables visualization of active nitrogen-fixing bacteria in specific gut regions. Coupled with histological examination, these methods provide detailed maps of microbial activity and its correlation with gut morphology and function.

Together, these approaches form a robust toolkit for investigating the role of nitrogen-fixing microorganisms in the digestive systems of rodents. Continued refinement and integration of these methods are vital for advancing our understanding of microbial contributions to nitrogen metabolism and the nutritional ecology of herbivorous rodents.

ECOLOGICAL AND NUTRITIONAL ROLE OF NITROGEN FIXATION IN THE DIGESTIVE TRACT OF RODENTS

Nitrogen is an essential element for all living organisms, playing a critical role in the synthesis of proteins, nucleic acids, and other cellular components. For herbivorous rodents, which primarily consume plant material often low in readily available nitrogen, maintaining adequate nitrogen intake is a constant nutritional challenge. Nitrogen fixation by symbiotic and free-living bacteria within the digestive tract offers a unique physiological adaptation that helps these animals compensate for nitrogen-poor diets (Zhou et al., 2022).

The nitrogen-fixing bacteria convert atmospheric nitrogen (N_2) into ammonia (NH_3), a form that can be assimilated by the host, thereby improving nitrogen availability and promoting growth, reproduction, and immune function. This symbiotic relationship may enhance the rodents' survival and fitness, especially in habitats where high-quality protein sources are scarce.

Furthermore, the enhanced nitrogen availability in rodent feces, enriched by microbial nitrogen fixation, has implications beyond the individual organism. As rodents deposit their feces into the environment, they contribute to the local nitrogen pool in the soil. This process may facilitate nutrient cycling and improve soil fertility, affecting plant growth and ecosystem productivity (Kohl and Dearing, 2014).

Population dynamics of rodents could also be influenced by nitrogen fixation capacity. Populations with more efficient nitrogen-fixing microbiota may better withstand periods of nutritional stress, potentially leading to greater population stability or growth. Additionally, these effects may influence interspecies interactions, such as competition and predation, as well as broader ecosystem processes.

Ecologically, rodents act as important ecosystem engineers and keystone species in many terrestrial habitats. Their burrowing, feeding, and fecal deposition behaviors directly affect nutrient redistribution and soil structure. Understanding the role of nitrogen fixation in their digestive tract adds a new dimension to their ecological significance, highlighting their contribution to biogeochemical cycles and ecosystem resilience.

Further research integrating microbial ecology, rodent physiology, and ecosystem science is crucial to fully elucidate these complex interactions and to harness this knowledge for conservation and sustainable management of terrestrial ecosystems.

PERSPECTIVES AND FUTURE RESEARCH DIRECTIONS

Despite significant advances in understanding nitrogen fixation within the digestive tracts of rodents, many questions remain unanswered. Current research often focuses on a limited number of rodent species and gut segments, leaving considerable gaps in our knowledge about the diversity and functionality of nitrogen-fixing microbial communities across different species, habitats, and seasons.

Addressing these gaps requires an interdisciplinary approach that integrates microbiological techniques with ecological field studies and physiological assessments. For example, combining high-throughput sequencing and metagenomics with stable isotope tracing and detailed nutritional analyses could provide a more comprehensive picture of nitrogen fixation dynamics and their impact on rodent biology.

Emerging technologies, such as single-cell genomics, metabolomics, and advanced imaging techniques, hold great promise for uncovering the specific microbial taxa involved, their metabolic pathways, and spatial distribution within the gut. Moreover, machine learning and bioinformatics can aid in analyzing complex datasets, facilitating the discovery of novel diazotrophs and their ecological roles.

From an applied perspective, understanding microbial nitrogen fixation in rodents may have significant implications for environmental sustainability and agriculture.

Rodents influence nutrient cycling and soil fertility, and their nitrogen-fixing symbionts could be harnessed to promote soil health and reduce the need for synthetic fertilizers. Additionally, insights into the microbiota of pest species might lead to innovative strategies for population control that are more environmentally friendly than traditional methods.

Finally, future research should also consider the effects of environmental changes, such as habitat alteration, climate change, and pollution, on the nitrogen-fixing microbial communities in rodent guts. Understanding how these factors affect nitrogen fixation could help predict ecosystem responses and guide conservation efforts.

CONCLUSION

Based on the presented data and previous research, it can be concluded that nitrogen fixation is a significant biological process present in various parts of the digestive system of both the red and common vole. Nitrogen-fixing activity was detected in both the tissues of the intestinal wall and in the intestinal contents, with the level of this activity being significantly higher in all intestinal segments compared to control groups. The most pronounced nitrogen fixation was observed in the wall of the large intestine, indicating the important role of this segment in the metabolic support and nutritional supplementation of rodents.

These results confirm the hypothesis that nitrogen-fixing bacteria, as part of the gut microbiota, can contribute to nitrogen mobilization in the vole's body, thereby compensating for the nutritional deficiencies of a diet rich in cellulose but poor in nitrogen. This provides an additional source of nitrogen that can be crucial for their growth, development, and survival in natural conditions.

Considering the importance of nitrogen fixation for the nutrition of herbivorous rodents, further research is necessary to gain a more detailed understanding of the microbiological mechanisms and specific bacterial species involved in this process. It is also essential to investigate the factors influencing the intensity of nitrogen-fixing activity in the digestive tract, as well as possible variations among different species and populations of rodents.

In a broader ecological context, the presence of nitrogen-fixing microorganisms in the intestines of voles may have a significant impact on the biogeochemical nitrogen cycles in soil, given their role in organic matter decomposition and contribution to the overall nitrogen cycling in ecosystems.

In conclusion, nitrogen fixation in the digestive tract of rodents represents an important yet insufficiently studied aspect of their biology and ecology, the understanding of which may have implications for other fields including agroecology, environmental protection, and rodent population management.

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