Journal of Tea Science Research, 2024, Vol.14, No.2, 57-63
http://hortherbpublisher.com/index.php/jtsr

Invited Review Open Access

Caffeine Degradation Pathways Mediated by Microbial Communities in Tea Fermentation

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Journal of Tea Science Research, 2024, Vol.14, No.2 doi: 10.5376/jtsr.2024.14.0006
Received: 07 Jan., 2024
Accepted: 11 Feb., 2024
Published: 02 Mar., 2024

Preferred citation for this article:
Zhang J., Huang B.F., and Xu G.M., 2024, Caffeine degradation pathways mediated by microbial communities in tea fermentation, Journal of Tea Science Research, 14(2): 57-63 (doi: 10.5376/jtsr.2024.14.0006)

Abstract The fermentation of tea is a complex biochemical process significantly influenced by the microbial communities present. This review paper focuses on the caffeine degradation pathways mediated by these microbial communities during tea fermentation. Understanding the mechanisms behind caffeine degradation is essential for optimizing tea processing to cater to varying consumer demands regarding caffeine content. This review comprehensively covers the role of microbial communities identified in different types of tea, such as Pu-erh, Oolong, and Black tea, and their specific interactions that lead to caffeine degradation. We discuss the involvement of key microorganisms, including various fungi and bacteria, and the enzymatic processes they facilitate. Special attention is given to the metabolic pathways of caffeine transformation, highlighting how specific microbes like Aspergillus sydowii and Lactobacillus casei contribute to these processes. Additionally, the paper examines environmental and processing factors that influence microbial activity and caffeine degradation. By synthesizing current research, this review aims to shed light on the potential of microbial engineering to develop tea products with controlled caffeine levels, thereby enhancing their health benefits and flavor profiles. Future research directions are suggested, focusing on the genetic and metabolic engineering of microbes to refine the caffeine degradation process further.
Keywords Caffeine degradation; Tea fermentation; Microbial communities; Microbial engineering; Enzymatic pathways

Tea, an infusion of the leaves of the *Camellia sinensis* plant, is one of the most widely consumed beverages in the world, second only to water. Its popularity is owed not only to its distinctive flavors and cultural significance but also to its numerous health benefits. Among the various bioactive compounds present in tea, caffeine is particularly notable for its stimulating effects on the human central nervous system, enhancing alertness and cognitive performance. However, the impact of caffeine on human health is complex, with studies indicating both beneficial and adverse effects depending on the context and level of consumption (Prasanth et al., 2019).

The process of tea fermentation, which is crucial in determining the flavor profile and chemical composition of the final product, involves a complex interplay between tea polyphenols and microbial communities. Microbial fermentation can significantly alter the levels of key metabolites in tea, such as catechins and caffeine, thereby influencing the sensory qualities and health properties of the beverage (Wang et al., 2023). The role of specific microbes, such as the "golden flower" fungi *Eurotium cristatum* and the fungus *Aspergillus sydowi*i, has been highlighted in the fermentation process, with implications for both the flavor and health benefits of the tea (Zhou et al., 2020a; Wang et al., 2023).

Understanding the pathways of caffeine degradation during tea fermentation is of particular interest, as it can lead to the production of metabolites with distinct health implications. For instance, the fungus *Colletotrichum camelliae* has been shown to metabolize caffeine through the degradation of uric acid, which may have applications in managing caffeine-contaminated environments and producing low-purine foods to prevent diseases like hyperuricemia and gout (He et al., 2023). Moreover, the microbial conversion of tea polyphenols and caffeine

by the human intestinal microbiota further underscores the complexity of tea's impact on health, with significant interindividual variability in metabolite profiles(Lee et al., 2006; Gross et al., 2010).

The purpose of this review is to explore the intricate pathways of caffeine degradation during tea fermentation, mediated by diverse microbial communities. By examining the metabolic and metagenomic analyses of these microbial interactions, we aim to shed light on the potential improvements in tea quality and the associated health benefits. This review will delve into the current state of knowledge on the subject, identify gaps in the literature, and suggest directions for future research.

1 Caffeine Degradation by Fungi in Tea Fermentation

1.1 Role of *Aspergillus sydowii* in caffeine degradation

Aspergillus sydowii has been identified as a significant fungus in the solid-state fermentation (SSF) of Pu-erh tea, with a notable capacity to degrade caffeine. Research has shown that when *A. sydowii* is inoculated into sun-dried green tea leaves for SSF, it has a profound effect on the tea's chemical composition, including amino acids, carbohydrates, flavonoids, and particularly caffeine metabolism (Zhou et al., 2020a). Metabolomic analysis using UPLC-QTOF-MS and HPLC has revealed that *A. sydowii* can promote the production of various compounds, including ketoprofen, baclofen, and tolbutamide, as a result of caffeine degradation (Zhou et al., 2020a). The primary pathway for this degradation appears to be demethylation, leading to the production of significant amounts of theophylline and other demethylated xanthines (Zhou et al., 2020a). Remarkably, *A. sydowii* has been shown to convert approximately 93.24% of degraded caffeine into theophylline, producing 27.92 mg/g of theophylline after fermentation (Zhou et al., 2020a). This demonstrates the potential of using *A. sydowii* as a starter strain for the controlled and efficient biosynthesis of theophylline during tea fermentation (Zhou et al., 2020a).

1.2 Comparative analysis with other fungi

The isolation and identification of caffeine-degrading microorganisms from Pu-erh tea have revealed a variety of fungi capable of degrading caffeine and its downstream metabolite, theophylline (Zhou et al., 2020b). Among these, *Aspergillus niger* and other *Aspergillus* species, such as *Aspergillus ustus* and *Aspergillus tamarii*, have been found to possess the ability to degrade theophylline in liquid culture (Zhou et al., 2020b). Comparative analysis of these fungi has shown that *A. ustus* and *A. tamarii* can degrade theophylline significantly, with *A. ustus* producing (129.48±5.81) mg/L of 3-methylxanthine and *A. tamarii* producing (159.11±10.8) mg/L of xanthine from theophylline in liquid medium (Zhou et al., 2020b). These findings suggest that different *Aspergillus* species have varying efficiencies in caffeine degradation and that they follow a similar N-demethylation pathway (Hakil et al., 1998; Zhou et al., 2020b).

In terms of efficiency, *A. sydowii* has been highlighted as particularly effective in converting caffeine to theophylline during SSF of Pu-erh tea (Zhou et al., 2019; Zhou et al., 2020a). In contrast, *A. niger*, while also capable of degrading caffeine, has been shown to enhance caffeine content and not significantly influence theophylline content under certain conditions (Zhou et al., 2019). This suggests that while both *A. sydowii* and *A. niger* are involved in caffeine degradation, *A. sydowii* may be more efficient in producing theophylline as a specific demethylated product (Zhou et al., 2019; Zhou et al., 2020a).

In conclusion, the role of *Aspergillus sydowii* in caffeine degradation during tea fermentation is significant, with the potential for practical applications in theophylline production. Comparative analysis with other fungi, such as *Aspergillus niger*, highlights the unique capabilities of *A. sydowii* and the importance of selecting appropriate starter strains for targeted metabolite production in fermented tea products (Zhou et al., 2019; Zhou et al., 2020a; Zhou et al., 2020b).

2 Caffeine Degradation Pathways

2.1 Demethylation as a primary pathway

The demethylation process is a critical pathway in the degradation of caffeine, particularly by the fungus *Aspergillus sydowii* during tea fermentation. Studies have shown that *A. sydowii* can significantly influence the metabolic profile of Pu-erh tea during solid-state fermentation (SSF), impacting not only caffeine but also amino acids, carbohydrates, and flavonoids. The utilization of UPLC-QTOF-MS and HPLC methods has revealed that *A. sydowii* facilitates the degradation of caffeine into demethylated metabolites such as theophylline and 3-methylxanthine. Remarkably, a substantial portion of the degraded caffeine, approximately 93.24%, is converted into theophylline, with a production of 27.92 mg/g after fermentation (Zhou et al., 2020a). Another study corroborates these findings, indicating that *A. sydowii* NRRL250 is capable of completely degrading caffeine in a liquid medium and significantly increasing the levels of theophylline and 3-methylxanthine as the primary degradation products (Zhou et al., 2018a).

2.2 Alternative degradation pathways

Exploration of caffeine degradation by various food microorganisms has revealed alternative pathways. A study focusing on the degradation of caffeine by *Lactobacillus casei*, *Leuconostoc mesenteroides*, *Rhizopus oryzae*, and *Saccharomyces cerevisiae* has demonstrated that these microorganisms can transform caffeine into dimethylxanthine and subsequently into methylxanthine. Notably, more than 89% of caffeine is converted into paraxanthine, which is then further transformed into either 1-methylxanthine by *L. casei* and *L. mesenteroides* or 7-methylxanthine by *R. oryzae* and *S. cerevisiae*. This indicates the presence of two distinct degradation patterns: the caffeine-paraxanthine-1-methylxanthine pathway and the caffeine-paraxanthine-7-methylxanthine pathway, with the former being utilized by *L. casei* and *L. mesenteroides* and the latter by *R. oryzae* and *S. cerevisiae* (Purwoko et al., 2023).

In summary, the primary pathway for caffeine degradation in *A. sydowii* involves demethylation, leading to the production of theophylline and 3-methylxanthine. However, alternative pathways exist in other food microorganisms, resulting in different patterns of degradation and metabolites. These findings are crucial for understanding the metabolic processes during tea fermentation and could have practical applications in controlling caffeine content and enhancing the production of specific metabolites in fermented tea products.

3 Optimization of Caffeine Degradation Conditions

3.1 Analysis of optimal conditions for caffeine degradation by *Aspergillus sydowii*

The degradation of caffeine by *Aspergillus sydowii* has been a subject of interest due to its potential application in the production of decaffeinated tea products. Research has identified *Aspergillus sydowii* NRRL250 as an effective strain for caffeine degradation in Pu-erh tea fermentation (Zhou et al., 2018a; Zhou et al., 2018b). The optimal conditions for caffeine degradation by this strain were determined through single-factor analysis, which revealed that a substrate concentration of 1,200 mg/L, a reaction temperature of 30 °C, and a pH of 6 were ideal for the process (Zhou et al., 2018a). Under these conditions, *A. sydowii* NRRL250 was capable of completely degrading 600 mg/L of caffeine in a liquid medium, and when applied to submerged fermentation of tea infusion, it degraded 985.1 mg/L of caffeine, producing 501.2 mg/L of theophylline (Zhou et al., 2018a).

3.2 Influence of substrate concentration, reaction temperature, and pH on degradation efficiency

The efficiency of caffeine degradation by *A. sydowii* is significantly influenced by substrate concentration, reaction temperature, and pH. A study demonstrated that varying the initial caffeine concentrations (600, 1,200, and 1,800 mg/L) affected the degradation products, with theophylline and 3-methylxanthine being the main products detected (Zhou et al., 2018b). The concentration of caffeine had a significant impact on the production of these degradation products, indicating that higher substrate concentrations could enhance the production of theophylline and 3-methylxanthine (Zhou et al., 2018b).

Temperature is another critical factor, with 30 °C being the optimum for *A. sydowii* NRRL250 to degrade caffeine (Zhou et al., 2018a). This temperature facilitates the metabolic processes of the fungus, allowing for efficient degradation of caffeine into its metabolites.

The pH of the medium also plays a crucial role in the degradation process. A pH of 6 was found to be optimal for *A. sydowii* NRRL250, which aligns with the slightly acidic conditions typically found in tea fermentation processes (Zhou et al., 2018a). This pH level supports the enzymatic activities necessary for the breakdown of caffeine molecules.

In conclusion, the optimization of caffeine degradation conditions by *Aspergillus sydowii* involves careful control of substrate concentration, reaction temperature, and pH, which are all critical factors that influence the efficiency of the degradation process and the production of valuable metabolites such as theophylline and 3-methylxanthine (Zhou et al., 2018a; Zhou et al., 2018b).

4 Impact of Microbial Fermentation on Caffeine Content

The impact of microbial fermentation on caffeine content in tea has been a subject of interest due to its implications for the flavor, health benefits, and commercial value of the final product. Recent studies have shed light on the complex interactions between microorganisms and caffeine during the fermentation process.

A study focusing on the use of single microorganisms during fermentation revealed that molds, particularly *Aspergillus niger* van Tieghem, significantly increased the caffeine content in green tea leaves. The caffeine content was observed to rise from an initial 3.47% to 9.63% by the 16th day of fermentation, marking an increase rate of 177.5%. This suggests that certain molds may have a unique ability to enhance caffeine levels, potentially through a biosynthetic route that differs from the one in tea plants, with theophylline being a possible precursor to caffeine in this microbial context (Wang et al., 2008).

In contrast, yeasts were found to decrease caffeine content during fermentation. This differential effect of molds and yeasts on caffeine levels indicates that the choice of microorganism in tea fermentation can be strategically used to control the caffeine content in the final product (Wang et al., 2008).

Aspergillus sydowii, another fungus with a high caffeine-degrading capacity, was studied for its role in the solid-state fermentation (SSF) of Pu-erh tea. The presence of *A. sydowii* in sun-dried green tea leaves led to significant changes in the tea's chemical composition, including amino acids, carbohydrates, flavonoids, and caffeine metabolism. Notably, *A. sydowii* promoted the production of theophylline through the demethylation of caffeine, with about 93.24% of degraded caffeine being converted to theophylline (Zhou et al., 2020a).

Furthermore, the microbial diversity in Xiaguan Tuo Tea during pile fermentation was investigated, revealing that fungi, particularly molds in the early stages and yeasts in the later stages, dominated the microbial population. This microbial activity resulted in a 59% increase in caffeine content by the end of the fermentation process (Li et al., 2018).

The role of food microorganisms in caffeine degradation was also explored, with *Lactobacillus casei*, *Leuconostoc mesenteroides*, *Rhizopus oryzae*, and *Saccharomyces cerevisiae* demonstrating the ability to reduce caffeine content in robusta beans. These microorganisms transformed caffeine into dimethylxanthine and then into methylxanthine, following two distinct degradation patterns (Purwoko et al., 2023).

In summary, microbial fermentation has a profound impact on the caffeine content of tea, with specific microorganisms either increasing or decreasing caffeine levels. Molds, particularly *Aspergillus species*, have been shown to increase caffeine content, while yeasts tend to decrease it. The choice of microorganism in the fermentation process can thus be a critical factor in determining the caffeine content and, consequently, the commercial and health-related properties of the tea (Wang et al., 2008; Li et al., 2018; Zhou et al., 2020a; Purwoko et al., 2023).

5 Practical Applications and Future Directions

The exploration of caffeine degradation pathways mediated by microbial communities in tea fermentation has revealed promising practical applications and highlighted areas for future research.

5.1 Potential use of specific microbial strains for controlled caffeine degradation in tea production

Recent studies have identified specific microbial strains capable of degrading caffeine, which could be harnessed to create tea products with controlled caffeine levels. For instance, *Aspergillus sydowii* has been shown to significantly degrade caffeine in Pu-erh tea through solid-state fermentation, converting a substantial portion of caffeine into theophylline via demethylation (Zhou et al., 2020a). Similarly, *Pseudomonas alcaligenes* FR 1708 has demonstrated the ability to completely degrade caffeine in solutions, suggesting its potential for application in decaffeination processes (Babu et al., 2005). The use of such strains in a starter culture could offer a more controllable and reproducible method for tea fermentation, with the added benefit of producing specific metabolites like theophylline (Zhou et al., 2018a; Zhou et al., 2020a).

5.2 Future research needs for understanding the complex interactions between microorganisms and caffeine metabolism

While the potential for microbial caffeine degradation is evident, there is a need for further research to understand the complex interactions between microorganisms and caffeine metabolism fully. Genetic characterization of caffeine degradation pathways has revealed two distinct mechanisms—N-demethylation and C-8 oxidation—employed by bacteria such as *Pseudomonas putida* (Summers et al., 2015). However, the influence of environmental factors, such as the presence of other carbon sources and pH levels, on the efficiency of caffeine degradation by microbes like *Pseudomonas* sp. GSC 1182, needs to be further explored (Gokulakrishnan et al., 2007). Additionally, the role of induced microbial cells in enhancing the degradation rate of caffeine presents an area ripe for investigation, as seen in studies involving *Pseudomonas* sp. (Gummadi et al., 2006).

The microbial diversity in tea fermentation, including the presence of yeasts and bacteria in Kombucha tea, also affects the biochemical properties of the beverage, such as its radical scavenging ability and caffeine degradation (Chakravorty et al., 2016). Understanding these dynamics could lead to optimized fermentation processes that enhance the beneficial properties of tea while reducing caffeine content.

In conclusion, the application of specific microbial strains for controlled caffeine degradation in tea production is a promising area for the tea industry. Future research should focus on the genetic and environmental factors influencing microbial caffeine metabolism, the optimization of fermentation conditions, and the broader implications of microbial activity on the health benefits of tea. This knowledge will be crucial for developing innovative tea products and fermentation techniques that meet consumer demands for lower caffeine content and enhanced health benefits.

6 Concluding Remarks

The exploration of caffeine degradation pathways mediated by microbial communities in tea fermentation has yielded significant insights into the metabolic processes involved. Research has identified two primary bacterial pathways for caffeine degradation: N-demethylation and C-8 oxidation. The genetic and enzymological foundations of these pathways have been elucidated, with genes responsible for N-demethylation found in Pseudomonas putida CBB5 and genes for C-8 oxidation in *Pseudomonas* sp. CBB1. Fungi, such as *Aspergillus sydowii* and *Aspergillus niger*, have also been shown to play a role in caffeine degradation during tea fermentation, with theophylline and 3-methylxanthine identified as key degradation products.

The implications of these findings are multifaceted. For the tea industry, understanding the microbial-mediated degradation of caffeine can lead to the development of novel fermentation processes that modulate caffeine content, potentially leading to new tea products with varying caffeine levels to meet consumer demands. This could also result in more economical methods for producing natural caffeine by leveraging microbial fermentation techniques.

From a consumer health perspective, the ability to control caffeine content in tea through microbial fermentation could cater to individuals sensitive to caffeine or those seeking low-caffeine alternatives for health reasons. Additionally, the production of theophylline, a compound with therapeutic applications, as a byproduct of caffeine degradation, presents potential health benefits and commercial opportunities.

In summary, the microbial-mediated caffeine degradation pathways in tea fermentation have significant implications for the tea industry and consumer health. The potential for creating customized tea products with desired caffeine levels and the possibility of producing health-beneficial compounds like theophylline could drive innovation and offer new avenues for tea consumption and application.

Funding

This work was supported by the Annual R&D Fund of Cuixi Academy of Biotechnology (grant No. 2024003).

Acknowledgements

We would like to thank Dr. Y. Zhou for his careful reading of this manuscript and for his revisions and polishing of the text. We are also grateful to the two anonymous peer reviewers for their serious and rigorous academic comments, which have greatly improved the quality of the paper.

Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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