

From nano- to macro-scale: a review of fungal-induced biomineralization mechanisms for self-healing and strengthening of materials

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ABSTRACT

Introduction. This review systematizes the key mechanisms of fungal-induced biomineralization for the self-healing and strengthening of mineral materials – calcium carbonate (CaCO_3) precipitation through urea hydrolysis and mycelial metabolic activity (FICP), as well as calcium oxalate (CaC_2O_4) formation via oxalic acid secretion (FIOP). **Materials and methods.** The review is based on an analysis of peer-reviewed scientific studies (Scopus, Web of Science), and more than 80% of them were published within the last five years (2022–2026). The analysis focused on qualitative and quantitative indicators of fungal impact on treated materials' properties – mineral composition and yield, strength gains, and reduced water absorption, confirmed by nano- and microscopy methods.

Results and discussion. A relationship between fungal species and strains, biomineralization mechanisms, medium compositions, and material strengthening effects has been identified in the study. It has been established that *Trichoderma reesei*, *Penicillium chrysogenum*, *Aspergillus niger*, and *Neurospora crassa* effectively induce carbonate biomineralization, enhancing self-healing and durability in concrete and soil matrices. *Pleurotus ostreatus* is considered a model organism capable of precipitating both calcium oxalates and carbonates, and forming bio-reinforcement that enables cyclic self-healing and strengthening of mineral material structures. However, implementing these biotechnologies requires developing application protocols and standards, as well as validation under real operating conditions. **Conclusion.** The present review provides a scientific base for further experimental developments and confirms the potential of fungal cultures for the self-healing and stabilization of mineral materials in construction, geotechnical engineering, and related fields.

KEYWORDS: biomineralization, biocementation, fungi, engineered living materials (ELM), microbially induced calcium carbonate precipitation (MICP, FICP), nanoscale, calcium oxalate, self-healing materials

SOURCES OF FUNDING FOR THE SCIENTIFIC WORK THAT RESULTED IN THE PUBLICATION: The research was funded by the National Research Moscow State University of Civil Engineering.

FOR CITATION:

Budnikova A.A., Topchiy D.V. From nano- to macro-scale: a review of fungal-induced biomineralization mechanisms for self-healing and strengthening of materials. *Nanotechnologies in Construction*. 2026; 18(4):507–520. <https://doi.org/10.15828/2075-8545-2026-18-4-507-520>. – EDN: RVMPIK.

От нано- до макроуровня: обзор механизмов биоминерализации с участием грибов для самовосстановления и упрочнения материалов

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АННОТАЦИЯ

Введение. В обзоре систематизированы ключевые механизмы биоминерализации, реализуемые грибной культурой, для самовосстановления и упрочнения минеральных материалов – образование карбоната кальция (CaCO_3) через гидролиз мочевины и метаболическую активность мицелия (FICP), а также оксалата кальция (CaC_2O_4) посредством секреции щавелевой кислоты (FIOP). **Методы и материалы.** Обзор основан на анализе рецензируемых научных публикаций (Scopus, Web of Science), из которых более 80% работ опубликованы за последние 5 лет (2022–2026 гг.). Внимание уделялось качественным и количественным показателям влияния грибов на характеристики укрепляемых материалов — составу и объему формирующихся минералов, приросту прочности и снижению водопоглощения, что подтверждалось методами нано- и микроскопии. **Результаты и обсуждение.** В ходе исследования выявлена взаимосвязь между видами и штаммами грибов, реализуемыми механизмами биоминерализации, составами питательных сред и эффектами упрочнения минеральных материалов. Установлено, что *Trichoderma reesei*, *Penicillium chrysogenum*, *Aspergillus niger* и *Neurospora crassa* эффективно индуцируют карбонатную биоминерализацию, обеспечивая самовосстановление и повышение устойчивости бетонных конструкций и грунтовых матриц. *Pleurotus ostreatus* рассматривается как «модельный» организм: он способен осаждать оксалаты и карбонаты кальция, а также формировать «биоармирование», что приводит к циклическому самовосстановлению и упрочнению структуры минеральных материалов. Однако для реализации описанных биотехнологий необходимы разработка методик и стандартов их применения, а также апробация в реальных условиях эксплуатации. **Заключение.** Настоящий обзор представляет научную основу для дальнейшего развития экспериментальных данных и подтверждает перспективы применения грибной культуры для самовосстановления и стабилизации минеральных материалов в строительной, геотехнической и смежных отраслях.

КЛЮЧЕВЫЕ СЛОВА: биоминерализация, биоцементация, грибы, инженерные живые материалы (ELM), микробно-индуцированное осаждение карбоната кальция (MICP, FICP), наноуровень, оксалат кальция; самовосстанавливающиеся материалы

ИСТОЧНИКИ ФИНАНСИРОВАНИЯ НАУЧНОЙ РАБОТЫ, РЕЗУЛЬТАТОМ КОТОРОЙ СТАЛА ПУБЛИКАЦИЯ: Данная работа выполняется в рамках реализации Программы развития федерального государственного бюджетного образовательного учреждения высшего образования «Национальный исследовательский Московский государственный строительный университет» на 2025–2036 годы.

ДЛЯ ЦИТИРОВАНИЯ:

Будникова А.А., Топчий Д.В. От нано- до макроуровня: обзор механизмов биоминерализации с участием грибов для самовосстановления и упрочнения материалов. *Нанотехнологии в строительстве*. 2026; 18(4):507–520. <https://doi.org/10.15828/2075-8545-2026-18-4-507-520>. – EDN: RVMP1K.

INTRODUCTION

Mineral materials underpinning the natural landscapes and urban built heritage suffer throughout their lifespan to physical, chemical, and biological weathering. Weak karst terrains (dolomite, limestone) are particularly hazardous due to their low water resistance and susceptibility to unpredictable collapses. These processes are intensified by human activity and climate change, underscoring the need for strategies to improve infrastructure durability and resilience, including heritage preservation [1–2].

In construction and materials science, there is an increasing focus on biotechnologies using bacteria and fungi capable of repairing structures through their metabolic activities, similar to wound healing in living systems [3–4]. In this context, the key process is biomineralization, whereby microorganisms precipitate calcium compounds, modifying the materials' composition, morphology, and structure [5–6].

Geomicrobiology and bioengineering research indicate the feasibility of fungal-mediated biomineralization under natural conditions. Fungi interact with rocks and

soil composites, promoting mineral formation across a wide range of conditions. Depending on substrate composition and metabolic activity, this phenomenon has a significant role in geochemical and biological cycles, altering the properties of soil and building structures [6–7].

The key biomineralization mechanism is microbially induced calcium carbonate precipitation (MICP), including bacterial- (BICP) and fungal-mediated processes (FICP) [8]. The effectiveness depends on the microorganism species, medium nutrients, calcium sources, inorganic carbon levels, acid-base balance (pH), nucleation sites (centers of crystal formation), as well as external factors like temperature, humidity, and weathering intensity [6–9].

In self-healing construction materials research, bacteria-mediated approaches (BICP) using *Bacillus pseudofirmus*, *Bacillus cohnii*, and *Sporosarcina pasteurii* are often encapsulated in biodegradable polymer capsules and mixed into cementitious matrices [10–11]. Upon crack formation (exposure to air and moisture), these microorganisms activate to precipitate calcite, enabling autonomous healing. However, bacterial methods demonstrate reductions in concrete compressive strength (up to 50%), since the pores in its matrix (0.5–1.5 μm) are smaller than the capsules (2–4 μm), which often leads to the development of voids in the material structure following capsule rupture [12]. Researchers also report limited microbial viability in alkaline environments (up to 2 months), high costs of nutrient medium components (primarily calcium lactate), and constraints on the width of healing cracks (up to 1 mm) [12–13].

Defining the nanoscale processes described above parameters is enabled for scientists by X-ray diffraction (XRD) and scanning electron microscopy (SEM) methods. XRD allows to determine the crystalline and molecular structure of the deposited minerals (for example, distinguishing calcite from aragonite) and the sizes of the precipitates, while SEM visualizes crystal morphologies and the distribution of crystals within the material. Meanwhile, Swedish studies show that combining SEM with energy-dispersive X-ray spectroscopy (EDX) and scanning-transmission X-ray microscopy (STXM) expands these methods' capabilities, enabling mineral distributions mapping and the fungal hyphae structure at the nanoscale (spatial resolution up to 30 nm) [14].

In this context, fungal biomineralization induced by the fungi *Trichoderma reesei*, *Penicillium chrysogenum*, *Aspergillus niger*, and *Neurospora crassa* (FICP) via urease-mediated hydrolysis and mycelial metabolism is regarded as a promising direction for advancing self-healing concrete technologies and soil biocementation [7–17]. These microorganisms remain viable in highly alkaline environments (pH 11–12) under extreme temperature

and humidity fluctuations, exhibiting calcium carbonate (CaCO_3) precipitation within short timeframes (the first precipitates observed after 12 hours) [12]. Moreover, fungal mycelium promotes intensive calcite crystal formation and distributes these crystals throughout the pores and cracks of structural elements as a result of its extended filamentous network and its numerous nucleation sites [12–17]. In addition, a high degree of compatibility has been observed between fungal metabolic products and the mineral-based materials matrix [17].

Beyond MICP–FICP, there is growing interest in creating living and high-strength biocomposites in which the mycelium serves both as a mineral-formation agent and a natural reinforcement [18–20]. *Pleurotus ostreatus*, an edible fungus, is of particular interest because it forms a flexible bioframework binding loose particles into a coherent structure, thereby enhancing the mechanical properties of mineral matrices [20–22]. It also promotes calcium oxalate deposition (CaOx , or CaC_2O_4) (FIOP), contributing to densification, surface hydrophobicity, and increased resistance to water erosion. These composites are environmentally friendly: biodegradable, recyclable, and associated with a lower carbon footprint. Depending on the processing method, fungal materials may exhibit a range of mechanical and technical characteristics, expanding their applications from packaging and thermal insulation to structural elements [20–23].

Despite the potential described above, the impact of strains and environmental conditions on mineral precipitation efficiency remains relatively underexplored [4, 9, 24, 25]. In existing studies, either a general mineralization mechanism is described without specifying fungal strains and medium composition; conversely, there is information about specifics of particular species but without nanoscale detailing of mineral formation and its evaluation (technology concept). This hinders optimization and scale-up of laboratory results.

This article aims to systematize the fungal-induced biomineralization mechanisms, identifying the specifics of calcium carbonate (FICP) and oxalate (FIOP) precipitation in relation to microorganism strains, nutrient medium composition, and the materials-strengthening effects. The findings will provide a basis for further research, refinement of fungal application methods for self-healing and stabilization of mineral materials (Fig. 1).

METHODS AND MATERIALS

The present review employs theoretical research methods — specifically, an analysis of peer reviewed publications indexed in Scopus and Web of Science. It is important to note that more than 80% of the works were published in the last five years (2022–2026), of which approximately 60% appeared in the last three years (2024–2026), underscoring the subject's relevance and

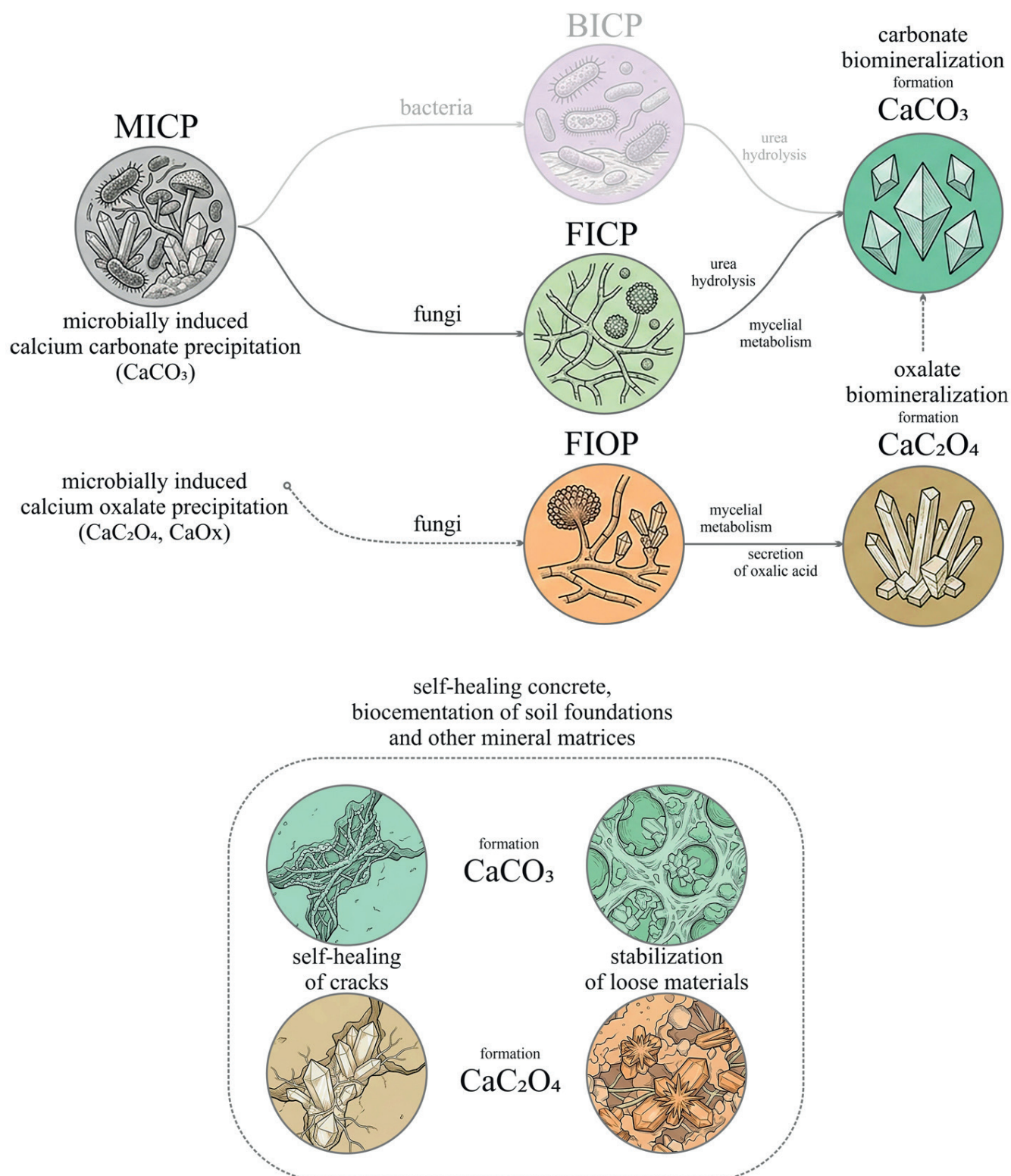


Fig. 1. The diagram of microbially induced calcium carbonate precipitation (MICP), including carbonate (FICP) and oxalate (FIOP) biomineralization mechanisms mediated by fungi for self-healing and strengthening of mineral materials

importance. The article also examines the findings of pioneering studies in the FICP field published over the past decade, which provides a solid basis and context for data comparison.

At the initial stage, approximately 100 works were reviewed to examine the fungal applications in the fabrication of high-strength biocomposites, self-healing systems, and engineered living materials (ELMs). Among them, more than 40 significant studies on self-healing and biocementation of mineral materials and soil foundations were identified.

The selection criteria included described biomineralization mechanisms, data on fungal species and strains, growth medium compositions, as well as quantitative and qualitative effects on the materials' functional properties: mineral precipitate composition and volume, strength gains, decreased water uptake, resistance to alkaline environments and moisture, and crack-healing capability. The special attention was paid to nano-structural analysis results and confirmation of the mentioned effects using nano- and microscopy methods (primarily SEM and XRD).

Acting as the keynote, the interrelation of the criteria underpins the review structure and determines the systematization logic. Furthermore, the author relied on their own scientific experience and experimental data obtained from work with the *Trichoderma* and *Pleurotus ostreatus* fungal strains. This enabled the preparation of a credible analytical synthesis that reflects current trends in the development of FICP and FIOP and ensures the integration of literature data with the author's research findings.

1. Carbonate biomineralization induced by fungi (FICP)

1.1. Calcium carbonate biomineralization based on urea hydrolysis (*Penicillium chrysogenum*, *Neurospora crassa*, *Aspergillus niger*)

The most studied biomineralization mechanism underlying microbially induced calcium carbonate precipi-

tation (MICP–FICP) is urea hydrolysis ($\text{CO}(\text{NH}_2)_2$), which produces ammonium (NH_4^+) and carbonate (CO_3^{2-}) ions [6, 8, 14, 17, 26]. In alkaline environments, these ions react with calcium (Ca^{2+}), leading to the formation of calcium carbonate (CaCO_3), which precipitates within the pores and cracks of building materials and soil matrices [17] (Fig. 2).

Among fungal species capable of urease-mediated biomineralization, *Penicillium chrysogenum*, *Neurospora crassa*, and *Aspergillus niger* have been the most extensively studied and discussed. They exhibit activity in mineral formation within cement slurry and confirm the reproducibility of results across diverse soil substrates [4, 8]. Swedish researchers conducted an experiment by sectioning the crystals precipitated by the fungi into thin plates with thicknesses of 75–200 nm. Scanning transmission X-ray microscopy (STXM) revealed that calcite, the most thermodynamically stable polymorph of CaCO_3 , formed on the hyphae of all tested microorganisms. In small amounts, nanocrystals of aragonite and calcium chloride (CaCl_2) were also detected, formed on extracellular polymeric substances (EPS) [14].

Chinese researchers demonstrated that the *Penicillium chrysogenum* CS1 strain promotes an increase in the compressive strength of river sand by 1.8 MPa during biomineralization, associated with CaCO_3 formation and binding of the material's particles [8, 17]. Meanwhile, replacing 20% of natural sand with waste-treated sand and *Aspergillus niger* contributed to an increase in compressive strength from 23 to 33 MPa and a reduction in water absorption from 0.9% to 0.5%. The authors attribute this effect to the fungal spores fixation in the pores of the cement-sand matrix and justify the prospects for applying this species in brick production [17, 27].

In an alternative study, the potential of *Penicillium chrysogenum* to precipitate calcium carbonate for biocementation of the surface layer of sandy soil and to reduce dust generation in arid (desert) regions is considered. In one experiment, the authors varied the concentrations of calcium chloride (CaCl_2) and urea ($\text{CO}(\text{NH}_2)_2$); in another, the inoculation methods for a fungal-based suspension were tested. The highest strength increases (over

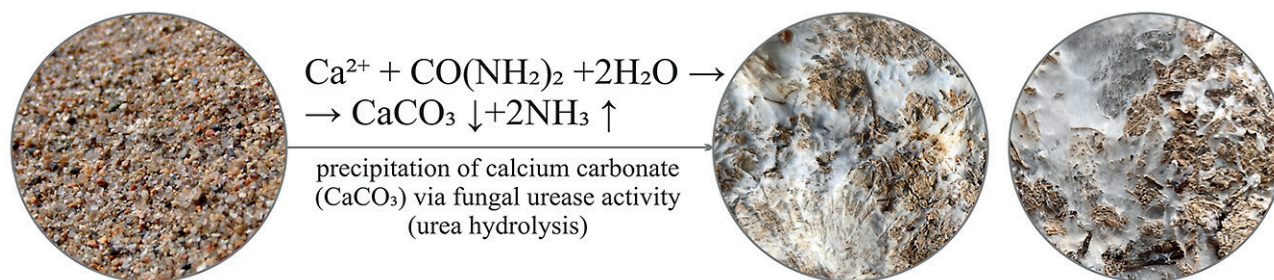


Fig. 2. Calcium carbonate biomineralization mechanism via urea hydrolysis and fungal urease activity: CaCO_3 formation and river sand samples biocementation

2.7 MPa) and carbonate contents were achieved within 24 hours when treating sand with solutions at 1.5 M CaCl_2 and 1.0 M $\text{CO}(\text{NH}_2)_2$. Scanning electron microscopy (SEM) confirmed calcite as the main mineral and enhanced soil particle adhesion at the nanoscale, indicating the possibility of forming durable soil foundations with the use of FICP [28].

Meanwhile, Portuguese researchers using *Penicillium chrysogenum* MUM 9743 and *Neurospora crassa* MUM 9208 to treat sand samples achieved a maximum compressive strength of 66.5 kPa. This may be due to differences in medium compositions and sand fractions, incubation conditions, and moisture levels [8].

Russian researchers point to the effectiveness of soil biocementation by the crossing of fungi and bacteria. Adding 2% paper waste (lignocellulosic substrate based on recycled paper) to soil, along with ureolytic *Bacillus licheniformis* DSMZ 8782 and the yeast-like fungus *Scytalidium candidum* 3C, created favorable conditions for calcium carbonate precipitation (CaCO_3) and increased the compressive strength from 61 kPa to 161.1 kPa. By the contrast, introducing biomass based only on fungi without cellulose and bacteria strengthened to 236.6 kPa, illustrating the fungi's potential for autonomous biocementation [29].

American researchers also studied the synergistic interaction between the widespread microscopic *Neurospora crassa* fungal mycelium and the *Sporosarcina*

pasteurii bacterium, developing an engineered living material (ELM) with self-healing and adaptation to harsh environmental conditions. In this system, the mycelium acts as a bioframework, and the bacteria create mineral deposits that reinforce the structure and contribute elasticity with moderate strength. The study demonstrated that *Neurospora crassa* hyphae can undergo self-mineralization without bacteria. However, the efficiency depends on the nutrient medium: the combination of urea and calcium drives the precipitation of calcium carbonate, along with reductions in dissolved components and improved strength, particularly under nitrogen deficiency. At the same time, the biomineralization process accelerated significantly when using *Sporosarcina pasteurii*, which within 24 hours almost completely hydrolyzed urea and calcium, demonstrating the potential of synergistic fungal–bacterial biosystems in creating self-healing construction materials as well as in soil strengthening and stabilization [29–30] (Fig. 3).

As a result, calcium carbonate biomineralization based on urea hydrolysis by *Penicillium chrysogenum*, *Neurospora crassa*, and *Aspergillus niger* demonstrates that fungi are effective agents for calcite formation. In addition to Ca^{2+} and urea, the provision of mineral nutrient sources and the inoculation process can provide substantial increases in the compressive strength of cement- and sand-based materials, accompanied by reductions in water absorption and improved soil stabilization.

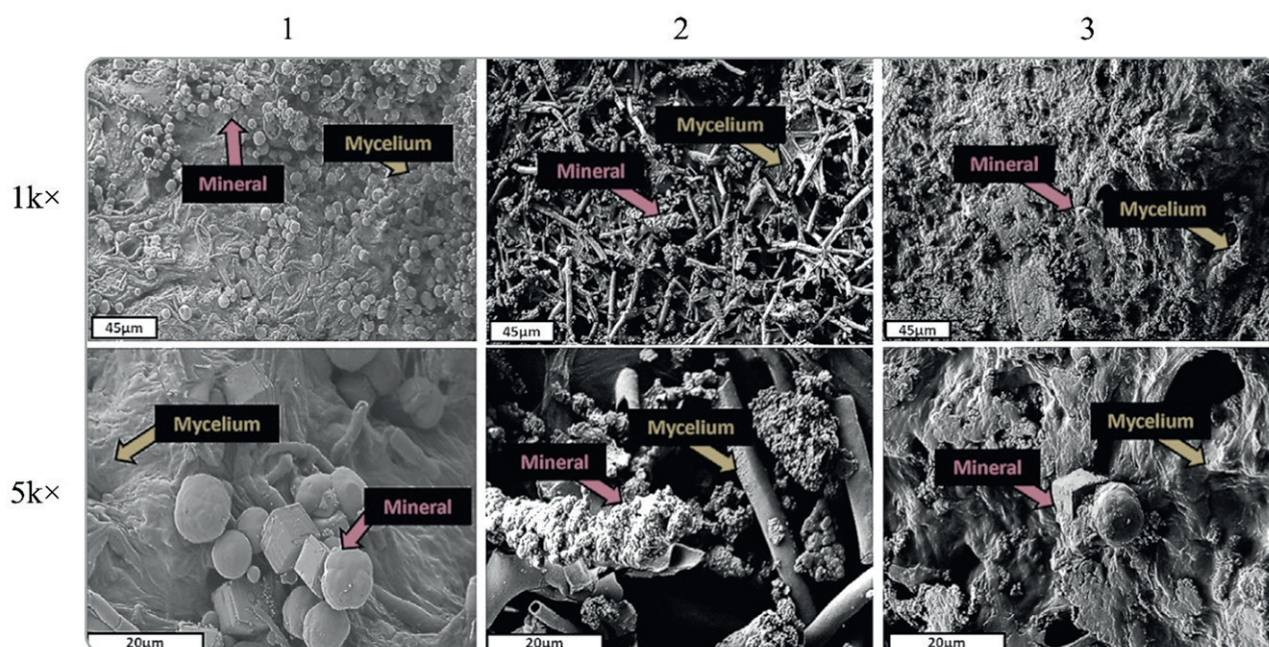


Fig. 3. Soil samples under biomineralization: calcium carbonate precipitation and mineral formation on fungal hyphae: 1 – control samples (without nutrient medium); 2 – experimental samples with urea; 3 – experimental samples incubated in malt medium. Images obtained by scanning electron microscopy (SEM) at magnifications of 1kx and 5kx. Scale bars: 45 μm (top row), 20 μm (bottom row) [30]

1.2. Calcium carbonate biomineralization based on fungal metabolic activity (*Trichoderma reesei*, *Candida ethanolica*, *Aspergillus nidulans*)

Some species of fungi are capable of calcium carbonate (CaCO_3) biomineralization without urease involvement: the mycelium deposits calcium ions (Ca^{2+}) during metabolism, consuming carbon dioxide (CO_2), which leads to the formation of carbonate ions and the deposition of minerals along the hyphal surfaces [31] (Fig. 4).

Studies by American scientists evaluate that *Trichoderma reesei* has a high potential for crack healing in concrete, as this species can adapt to harsh environmental conditions such as low humidity, extreme temperatures, ultraviolet radiation, and high alkalinity [12–13, 32]. In their experiments, the researchers compared the effectiveness of *Trichoderma reesei*, *Aspergillus nidulans*, *Cadophora interclivum*, *Umbeliopsis dimorpha*, *Acidomelania panicola*, and *Pseudophialophora magnispora* in CaCO_3 formation in potato-dextrose agar-based media. Despite leaching of calcium hydroxide $\text{Ca}(\text{OH})_2$ from the cementitious composition and a sharp pH rise from 6.5 to 13.0, *Trichoderma reesei* demonstrated sustainable growth on and off the concrete surface, while other fungi showed no activity [12]. X-ray diffraction (XRD) and scanning electron microscopy (SEM) showed that the crystals precipitated on the fungal hyphae consist of calcite. The first carbonate formations were detected after 12 hours, and their widespread distribution was observed by day 21. Concurrently, it was established that concrete compressive strength increases with spore content of 5×10^6 cells/mm³, but deviations from this baseline reduce the effect [12]. In other studies, it was shown that a ratio of 8.42 g of *Trichoderma reesei* spores per 1 liter of potato-dextrose agar-based suspension provides maximum concrete compressive strength of 18.99 MPa after 28 days, indicating the need to adhere to strict dosing ranges of fungal culture in compositions [33].

Russian researchers have developed methods for healing and strengthening stone structures and karst limestone soils using a substrate based on natural components and

Trichoderma fungal spores. This approach maintains microorganism viability within cracks, promoting calcium carbonate precipitation during metabolism for self-healing of material with similar composition. As a result, stone structures can double in strength, reaching up to 40 MPa within 28 days without human or technological intervention [34–35]. The technology ensures self-healing of mineral materials and prevents unpredictable destruction and collapses of soils, demonstrating the practical and ecological potential of FICP in infrastructure reinforcement [20, 31, 35].

Malaysian scientists, in turn, showed that the *Candida ethanolica* yeast-like fungus, under a specific nutrient medium composition and Ca^{2+} concentration, promotes an increase in concrete compressive strength by 6.27% relative to control samples, reaching 32.2 MPa after 28 days. The precipitated CaCO_3 also reduces concrete water absorption and enhances its resistance to environmental impacts [6, 17, 36].

Filamentous fungus *Aspergillus nidulans*, although capable of hydrolyzing urea, demonstrates the ability for biomineralization in an alkaline concrete environment even without urease. For these purposes, mutant strains (for example, MAD1445) are utilized: they are able to grow on concrete slabs surfaces under high pH, and precipitate CaCO_3 when calcium is added to the medium [17, 37].

As a result, calcium carbonate biomineralization based on fungal metabolic activity requires not only calcium sources but also nutrients (including trace elements), facilitating autonomous precipitation of CaCO_3 in alkaline environments and supporting the development of sustainable infrastructure [38–39].

2. Oxalate biomineralization induced by fungi (FIOP)

2.1. Oxalate biomineralization via secretion of oxalic acid (*Aspergillus niger*, *Penicillium spp.*, *Abortiporus biennis*)

Oxalate biomineralization is a distinct mineral formation mechanism carried out by fungal culture. In neu-

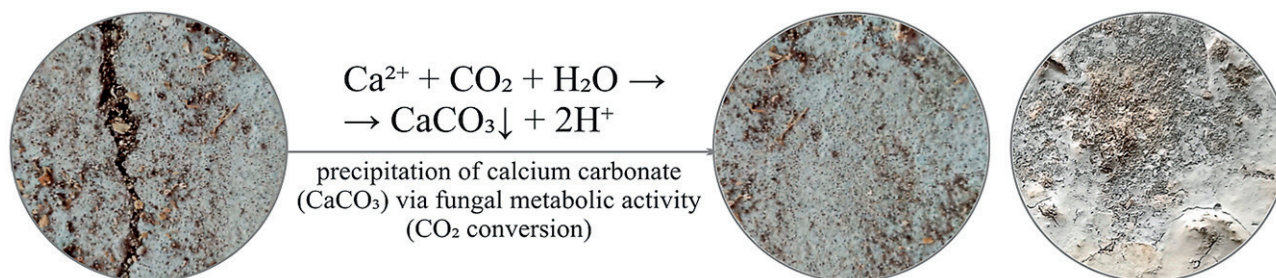


Fig. 4. Calcium carbonate biomineralization mechanism via fungal metabolic activity and conversion of carbon dioxide: CaCO_3 formation and self-healing of concrete

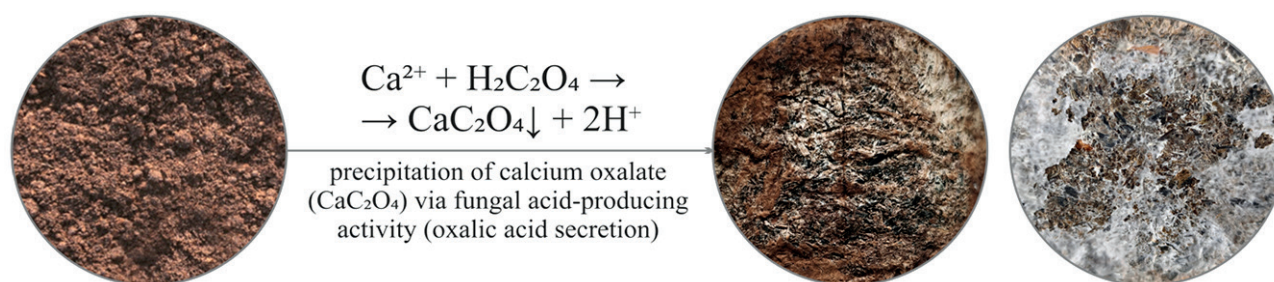


Fig. 5. Oxalate biomineralization mechanism via fungal oxalic acid secretion: CaC_2O_4 formation and soil foundations stabilization

tral and alkaline environments, oxalic acid ($\text{H}_2\text{C}_2\text{O}_4$), secreted by fungi, interacts with calcium ions (Ca^{2+}) to produce calcium oxalate (CaC_2O_4 or CaOx) — a poorly soluble salt that precipitates on hyphal surfaces. This oxalate can undergo biotic (for example, bacterial activity) and abiotic transformations, releasing carbonate ions and resulting in calcium carbonate (CaCO_3). In this process, CaOx acts as an intermediate step in calcium carbonate biomineralization [8, 24, 42]. Moreover, studies by British researchers have proven that oxalic acid secreted by fungi can further interact with the CaCO_3 formed, releasing carbonate ions and inducing its cyclic precipitation [8, 43] (Fig. 5).

Polish and Russian researchers established that *Aspergillus niger* and *Penicillium spp.* realize oxalate biomineralization when calcium is present in the substrate. Moreover, the process rate and intensity increase when acidic constituents are added to the medium to neutralize the pH [24, 42]. It was also noted that *Abortiporus biennis* is capable of simultaneously forming oxalates and binding heavy metals, which facilitates their immobilization and demonstrates the fungus's tolerance to polluted environments [4, 24].

Thus, oxalate biomineralization creates prerequisites for the subsequent formation of calcium carbonates (CaCO_3). Moreover, it represents an autonomous mechanism — a significant biogeochemical process that ensures the cyclic self-healing and immobilization of toxic elements in natural and artificial environments.

2.2. Oxalate biomineralization and mycelial bioreinforcement (*Pleurotus ostreatus*)

Research by Russian scientists indicates that *Pleurotus ostreatus* — based biotechnologies represent a promising approach to strengthening mineral materials prone to decay. This mycelium exhibits metabolic and physical flexibility, allowing it to adapt to extreme conditions, modify substrate properties depending on the processing method (increasing material strength by 2–6 times), and form self-healing, elastic, and environmentally friendly biocomposites [20]. Experiments demonstrate that *Pleurotus ostreatus* mycelium is capable of forming both oxalate and calcium carbonate; acting as a material natural reinforcement, providing cyclic healing and strengthening of soil foundations over 90 days (1 cycle — 28 days) [20] (Fig. 6).

Studies by Chinese researchers confirm that *Pleurotus ostreatus* induces oxalate biomineralization, substantially improving the physical and mechanical properties of sandy soils. Experiments demonstrate that the mycelium binds surface particles, preventing water erosion even under intense mechanical mixing (120–170 rpm). The increase of the contact angle to 116.42° also indicates surface hydrophobization, thereby increasing the material's resistance to hydrodynamic loads [8, 44].

Microscopic analysis of mineral precipitates indicated they consist mainly of calcite, as well as calcium oxalate monohydrate ($\text{CaC}_2\text{O}_4 \cdot \text{H}_2\text{O}$) and dihydrate ($\text{CaC}_2\text{O}_4 \cdot 2\text{H}_2\text{O}$) [8]. Micro- and nano-scale studies con-

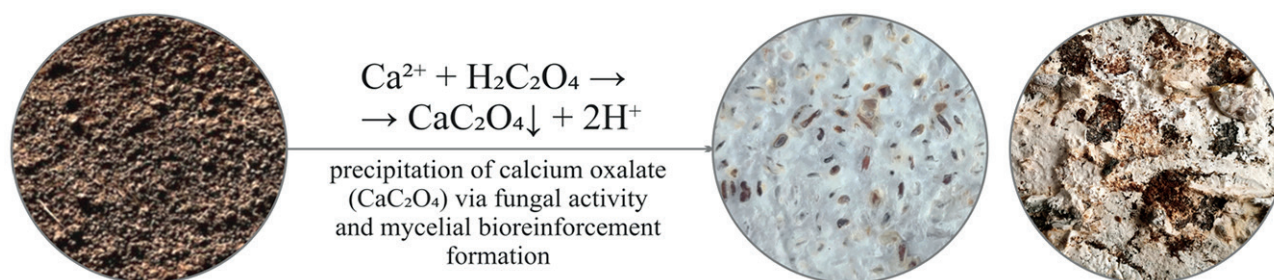


Fig. 6. Oxalate–carbonate biomineralization mechanism with *Pleurotus ostreatus*: CaCO_3 and CaC_2O_4 formation, mycelial bioreinforcement and strengthening of soil foundations

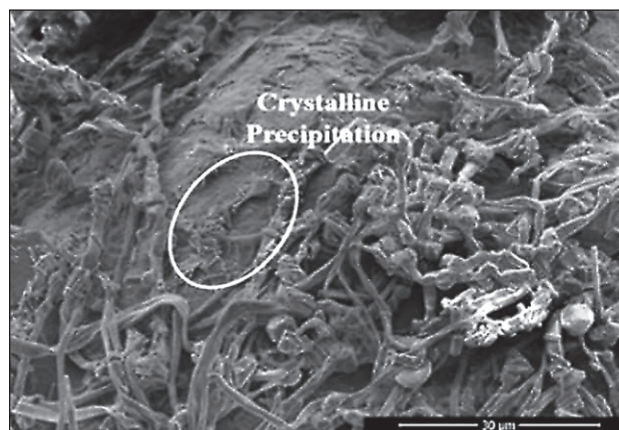
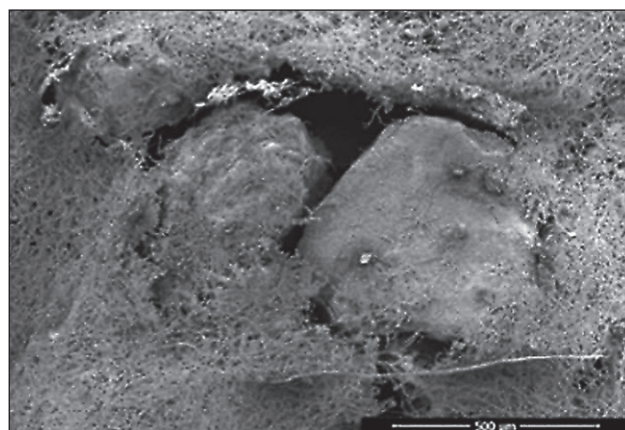


Fig. 7. Image of a sandy layer biocemented with *Pleurotus ostreatus*, obtained by scanning electron microscopy, demonstrated the mycelial framework and precipitated minerals (SEM) [8]

firmed the sequential biomineralization nature: fungal metabolic activity is linked to the oxalic acid secretion, which leads to a local pH drop and the oxalates precipitation on fungal hyphae. In the subsequent stages, oxidative processes or a rise in pH may convert oxalates into calcium carbonate, enabling cyclic remineralization of pores and cracks in materials and soil matrices [8, 44] (Fig. 7).

As a result, *Pleurotus ostreatus* induces the calcium oxalate (CaOx) and carbonate (CaCO₃) precipitation, forming a bioframework that leads to structural self-healing and strengthening of mineral materials. It is regarded as a model organism, demonstrating the capabilities of fungal culture in biomineralization and bioreinforcement [20, 22, 31, 35, 44].

RESULTS AND DISCUSSION

The present review demonstrates that fungal-induced biomineralization represents an independent and promising area in the development of engineered living materials—durable, environmentally friendly, and self-healing. Fungi not only facilitate calcium carbonate (CaCO₃) and oxalate (CaOx) precipitation but also act as biological reinforcements through their hyphal structure. This has a positive effect on the materials strength, porosity, and water resistance, as confirmed by experimental data from nano- to macro- scales.

A comparative analysis of calcium carbonate biomineralization based on urea hydrolysis and fungal metabolic activity evaluates that both processes efficiency depends on the fungal species and strains, key nutrient medium components (urea, cellulose, etc.), and the calcium sources (Ca²⁺ or calcium salts like as CaCl₂). Experimental results indicate high efficacy of certain fungi in strengthening mineral-based materials over 28 days: *Trichoderma reesei* (increase in concrete and karst soil strength up to 40 MPa), *Aspergillus niger* (strength gain in cement-sand mixes from 23 to 33 MPa with reduced water absorption

from 0.9 to 0.5%), *Candida ethanolica* (strength increase by 6.27% to 32.2 MPa), as well as *Penicillium chrysogenum* and *Neurospora crassa* (soil strength increases by 1.8 to 2.7 MPa). Additional studies demonstrate that *A. niger*, *P. chrysogenum*, and *A. biennis* are capable not only of mineral precipitation but also of heavy metal immobilization.

Pleurotus ostreatus, in turn, promotes calcium oxalate (CaOx) precipitation with transformation into calcium carbonate (CaCO₃), acting as a natural bioframework of materials; this leads to cyclic and structural self-healing and strengthening of mineral matrices. This genus can be considered a model organism due to the broad potential in biomineralization and biological reinforcement, opening prospects for further research and development of methods to utilize *Pleurotus ostreatus* for strengthening a wide range of mineral materials.

However, there are significant discrepancies between results, which may be due to differences in strains and experimental conditions. Additionally, mechanisms of encapsulation and long-term viability of fungi within cementitious matrices, their resilience to cyclic moisture and temperature fluctuations, as well as the reproducibility of self-healing effects under real-world conditions, are still insufficiently studied.

Despite the fact that the direction of mineral deposition and concrete restoration using fungal culture (FICP) has been under investigation for about 10 years (since 2016–2019), significant progress has already been made. Important tasks for future research include standardized selection of the most stable and effective fungal strains for specific materials, development of encapsulation methods that preserve viability without reducing the material's baseline strength, and advancement of synergistic MICP–FICP systems through fungal–bacterial co-cultures.

Therefore, it is necessary to develop standards and application protocols for fungi-based self-healing and reinforcement, as well as unified criteria for evaluating

biomineralization effectiveness to enable scaling from laboratory studies to engineering macro-scale systems.

This work presents the relationships between fungal species and strains, the biomineralization mechanisms realized, the nutrient media compositions, and the effects on strengthening mineral materials. The review provides a comprehensive overview of the current tech-

nological potential of living fungal cultures for biomineralization, identifies limitations scaling limitations, and lays a scientific foundation for further experimental data development, confirming the prospects applying fungal cultures for self-healing and stabilization of mineral materials in construction, geotechnical, and related industries (Table 1).

Table 1. Fungal-induced biomineralization mechanisms: the relationship between species and strains, biomineralization mechanisms, media compositions, and the output properties (effects) of treated materials

Fungal species and strains	Biomineralization mechanism	Nutrient medium	Strengthened material and effects	Level of study and practical potential
<i>Penicillium chrysogenum</i> (CS1, MUM 9743)	– Carbonate biomineralization based on urea hydrolysis; – Oxalate biomineralization based on oxalic acid secretion	Urea, calcium sources / Ca^{2+} salts (CaCl_2 , etc.)	Sandy soils: increase in compressive strength by 1.8–2.7 MPa, CaCO_3 formation between particles	Biocementation effect on sandy soil surfaces was demonstrated
<i>Neurospora crassa</i> (MUM 9208)	– Carbonate biomineralization based on urea hydrolysis	Urea, calcium sources / Ca^{2+} salts (CaCl_2 , etc.), nutrient base for engineered living materials (ELM)	Sandy soils: increase in strength by 66.5 kPa, in ELM – CaCO_3 and bio-reinforcement formation	Promising component for ELM, creating bioreinforcement and mineral distribution in matrices
<i>Aspergillus niger</i>	– Carbonate biomineralization based on urea hydrolysis; – Oxalate biomineralization based on oxalic acid secretion	Urea, calcium sources / Ca^{2+} salts (CaCl_2 , etc.)	Cement-sand mixes with molding sand and waste materials: increase in strength from 23 to 33 MPa; reduction in water absorption from 0.9% to 0.5%	Promising component for modified cement-sand composites, further studies are needed on reproducibility and biosafety (pathogenicity)
<i>Abortiporus biennis</i>	– Oxalate biomineralization based on oxalic acid secretion	Calcium sources (Ca^{2+}), microelements	Soils composites: immobilization of heavy metals	Promising component for bioremediation due to resistance to toxic conditions
<i>Scytalidium candidum</i> (3C)	– Carbonate biomineralization based on urea hydrolysis	Urea, CaCl_2 , <i>Bacillus licheniformis</i> DSMZ 8782 (optional), recycled waste paper (lignocellulose)	Sandy and other soils: increase in strength up to 161.1 kPa with bacteria, up to 236.6 kPa with fungal substrates	Promising component for soil stabilization and ground improvement, biosafety assessment is required (pathogenicity of candidum)
<i>Trichoderma reesei</i>	– Carbonate biomineralization based on fungal metabolic activity	Potato dextrose agar (PDA/PDB), calcium sources / salts (CaCl_2 , calcium lactate), mineral components	Concrete: CaCO_3 formation in cracks, effectiveness in alkaline environments, strength gain up to 18.99 MPa. Rock and karst soils: strength doubled to 40 MPa in 28 days	One of the most studied fungi, promising for self-healing concrete and soil stabilization
<i>Candida ethanolica</i>	– Carbonate biomineralization based on fungal metabolic activity	Nutrient medium, calcium sources / Ca^{2+} salts (CaCl_2 , etc.)	Concrete surface: strength increased by 6.27% to 32.2 MPa, CaCO_3 layer formation	Promising component for surface strengthening of concrete, biosafety assessment is needed (pathogenicity of candida)
<i>Aspergillus nidulans</i> (MAD1445)	– Carbonate biomineralization based on fungal metabolic activity	Potato dextrose agar (PDA/PDB), calcium sources / salts (CaCl_2 , calcium lactate)	Concrete slabs: maintains viability at pH 13, CaCO_3 precipitation	Promising mutant model for improving mechanisms and methods
<i>Pleurotus ostreatus</i> (M5)	– Oxalate biomineralization based on fungal metabolic activity – Carbonate biomineralization based on fungal metabolic activity – Mycelial bioreinforcement (bioframework)	Natural components, calcium sources / Ca^{2+} salts	Sandy and calcareous karst soils: formation of CaOx and CaCO_3 , surface hydrophobization, cyclic self-restoration, and strengthening for 90 days	Promising component and model organism demonstrating fungal capabilities in biomineralization and bio-reinforcement, high potential for soil stabilization and forming high-strength, eco-friendly biocomposites

CONCLUSION

Fungal-induced biomineralization represents a promising direction in the development of engineering living materials as well as technologies for self-healing and strengthening mineral-based composites. This review systematizes two key mechanisms: calcium carbonate (CaCO_3) formation via urea hydrolysis and fungal metabolic activity (FICP), and calcium oxalate (CaC_2O_4) precipitation through oxalic acid secretion (FIOP).

The study identified relationships between fungi species and strains, biomineralization mechanisms, nutrients media compositions, and effects on the strengthening of mineral materials. It has been shown that *Trichoderma reesei*, *Penicillium chrysogenum*, *Aspergillus niger*, and *Neurospora crassa* effectively induce calcium carbonate formation, increasing the strength and water resistance of concrete and soil materials. *Pleurotus ostreatus* demon-

strates the ability to precipitate both calcium oxalate and carbonate, as well as to create bioreinforcement, enabling cyclic self-healing and strengthening of mineral matrices.

Experimental data at nano- and macro-scales confirm the positive impact of fungi on enhancing the materials' operational properties, supporting the potential application of these cultures in construction, geotechnical, and related industries. Nonetheless, there is a need for standardization of fungi application methods for self-healing and reinforcement, development of encapsulation systems within existing matrices, establishing evaluation criteria for biomineralization efficiency, and testing system stability under real service conditions.

In this regard, the present article provides a scientific basis for further research and confirms the high potential of fungal cultures in consolidating and self-healing mineral materials for construction, geotechnical, and related fields.

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ADDITIONAL INFORMATION

The authors declare that generative artificial intelligence technologies and technologies based on artificial intelligence were not used in the preparation of the article.

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The authors declare no conflicts of interests.

The article was submitted 06.07.2026; approved after reviewing 13.08.2026; accepted for publication 18.08.2026.