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Mechanisms of Biodeterioration of Structural Materials by *Streptomyces* spp.: A Review †

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Abstract: The processes of microbial damage to materials lead to a number of environmental problems. To prevent the development of eco-trophic corrosively active groups of micro-organisms, "green" biocides/inhibitors are being developed. Actinobacteria of the genus *Streptomyces* are actively studied from the point of view of usefulness/harmfulness in relation to human activity, in particular, in the processes of microbial damage to materials. To summarize the results of available scientific research and reviews devoted to the participation and supposed mechanisms of structural materials damage caused by streptomycetes, the presented study was performed. The possible role of streptomycetes in the biodeterioration of structural materials was speculated. The obtained data indicate the need for further studies on streptomycetes as participants in the corrosion process, with special attention to their production of secondary metabolites and nanoparticles of metal and metal oxides with antimicrobial and inhibitory properties, which will contribute to the expansion of the list of "green" biocides/inhibitors.

Keywords: *Actinobacteria*; construction materials; "green" biocides/inhibitors; mechanisms of biodeterioration; *Streptomyces*

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1. Introduction

The processes of the biodegradation of materials, harmful from the point of view of practical human activity, are considered through their biodamage, which should be prevented and eliminated. Material deterioration leads to a number of environmental problems [1]. Biocides/inhibitors used to protect against corrosion, including microbial corrosion, are often toxic compounds [2,3]. Eco-friendly "green" biocides/inhibitors are being developed today based on the requirements of ensuring the preservation of the quality of the environment [3–5]. It is known that representatives of the genus *Streptomyces* play an active part in the destruction of materials: wall paintings suffer from the growth and colonization of *Streptomyces* [6,7], the biodegradation of rubber latex occurs with the participation of *Streptomyces* labedae isolated from the soil [8], and streptomycetes have been isolated from damaged film and oil-bitumen coatings of gas pipelines and underground tanks [9,10]. At the same time, sulfate-reducing and thione bacteria are considered the main corrosively active groups of micro-organisms [10–12]. Streptomycetes are considered as heterotrophic bacteria companions of the main groups of material damagers [13].

A study of the diversity, richness, and composition of microbial communities on a steel surface in marine conditions showed that Proteobacteria accounted for 83.1% of the total, *Firmicutes* was 6.3%, *Actinobacteria* was 3.2%, and *Bacteroidetes* was 2.8% [14]. In soils, *Streptomyces* is the most common genus of *Actinobacteria*—consisting of almost 70% of the total [15].

Mechanisms of microbiologically influenced corrosion (MIC) proposed by researchers, related to SRB activity and developed for anaerobic environments, are reviewed and improved [16]. Currently, the most likely mechanisms of MIC comprises several theories [16]: 1. theory of cathodic depolarization; 2. theory of sulfides; 3. theory of uptake electrons (in particular, redox mediators) by micro-organisms; and 4. the participation of micro-organisms in the formation of the mineralogical composition of biofilms on the materials' surfaces.

Furthermore, there is also the mechanism proposed by Moura et al. [17], who observed the acid produced by bacteria and their formation of corrosive media. *Streptomyces* is also able to oxidize sulfur compounds and produce sulfuric acid [18].

Moreover, streptomycetes are also well-known for properties such as the production of enzymes, antibiotics, and other metabolites with biological activity [19–22] which are suggested to produce "green" corrosion inhibitors [23–25] and are used for biocontrol in agricultural technologies [26,27]. Synthesizing various enzymes, representatives of this genus can be used for biotransformation processes [28].

Parthipan et al. [29] suggested that a detailed analysis and understanding of microbial communities involved in the biocorrosion processes of steel is required with particular attention to the features and properties of bacteria of the family *Streptomycetaceae*.

To summarize results of available scientific research and reviews devoted to the participation and supposed mechanisms of structural materials biodamage, caused by streptomycetes, the presented study was performed. Here, we present a concise review of published information on the ability of streptomycetes to develop a biofilm, as a component of microbial association and as a pure bacterial culture, and their involvement in the corrosive process, induction, and possible MIC prevention. We consider streptomycetes, well-known metabolite producers, as biocides/inhibitors, and suggest using their secondary metabolites for this purpose. Finally, we discuss challenges and potential directions for future research and present a general outline of the involvement of *Streptomyces* spp. in MIC processes.

2. Streptomycetes and Biofilm

Streptomycetes are aerobic, gram-positive, acid–alcohol-labile bacteria that form a widely branched substrate mycelium that rarely fragments and belongs to the phylum *Actinobacteria*. Mature aerial mycelium forms chains of three to many spores. Members of several species bear short chains of spores on the substrate mycelium. The configuration of spore chains (or sporophores) has played a very important role in species descriptions for many years [30]. Phenotyping methods are widely used in their identification [31]. At the same time, the identification of representatives of the genus *Streptomyces* is problematic, since identical 16S rRNA sequences have been established in species where the strains differ in phenotype, morphology, and biochemistry [32]. The researchers note that the best available method for identifying *Streptomyces* species is whole-genome sequencing [33].

Streptomycetes are part of the soil microbiome [34], playing a significant role in soil properties and fertility. Soil microbiomes cause material deterioration through biofilm formation [35,36], including the microbiologically influenced corrosion of metals [10,37]. Actinobacteria (including *Streptomyces* spp.) are one of the bacterial groups that has the ability form a biofilm [38,39]. The cycle of biofilm development is believed to include [40]: 1. Initial attachment of microbes to a surface or to each other—most often, micro-organisms exist as free-floating masses or single (eg., planktonic) colonies. However, under normal conditions, most micro-organisms tend to attach to the surface and eventually form a biofilm; 2. Formation of microcolonies—as bacteria multiply, they stick more firmly to the surface, differentiate, and exchange genes, which ensures their survival; 3. Biofilm maturation—once firmly attached, the bacteria begin to form an exopolysaccharide surrounding matrix known as extracellular polymeric substance. This is a protective matrix or "slime". Small colonies of bacteria then form an initial biofilm; 4. Dispersal (spread) of the biofilm.

It was suggested that streptomycetes, as representatives of *Actinobacteria*, can participate in MIC-forming biofilm. The formation of a biofilm by *Streptomyces parvus* (*S. parvus*) strain B7 is considered due to its involvement in the corrosion of steels [41]. Volkland et al. [42] showed that in the presence of *Streptomyces pilosus* (*S. pilosus*) strain DSM 40714 (which does not form a biofilm) and phosphates, the corrosion rate reduction in mild steel 37/AISI 10-18 in mineral media does not occur.

On the other hand, an approach using bacterial biofilms to combat corrosion is being developed [43]. The absence of the ability to inhibit the corrosion process of steel (SAE 1018) has been defined for *Streptomyces lividans* (*S. lividans*) strain TK24, which does not form a biofilm [44]. As a conclusion, the authors note that corrosion inhibition is due to the living cells of the biofilm. *S. lividans* strain TK23.1, having poor biofilm formation, showed the same degree of MIC of steel SAE 1018 as in the control without bacteria [45]. Bleich et al. [46] noted that thiocillin (an antibiotic belonging to the group of thiopeptides) promotes the growth of the matrix-producing *B. subtilis* population on the plastic of microplates. Therefore, thiazolyl peptides (thiopeptides) deserve attention as stimulators of biofilm formation. Since *S. gardneri* is known to produce thiazolyl peptides (thiopeptides) [47], attention should be paid to studying the participation of this species in MIC. However, for *S. gardneri* strain ChNPU F3, antagonistic and antibiofilm properties were shown against *Bacillus simplex* strain ChNPU F1 [48]. At the same time, the specified strains are moderately adhesive in terms of their ability to form a biofilm [49]. The authors hypothesize their involvement in material damage by producing corrosion/anticorrosion metabolites, but not by biofilm formation.

Information on the formation of biofilms by streptomycetes and their involvement in MIC processes is presented in Table 1.

Table 1. Biofilm-forming ability of streptomycetes and MIC processes.

Species	Biofilm-Forming Ability	Secondary Metabolites with Antimicrobial Activity/ Antagonistic Activity	Corrosive Activity	References
S. parvus strain B7	powerful	not specified	yes	[41]
S. pilosus strain DSM40714	poor	not specified	yes	[42]
S. lividans strain TK24	poor	not specified	yes	[44]
S. lividans strain TK23.1	poor	not specified	yes	[45]
S. gardneri strain ChNPU F3	poor	yes	not specified	[48,49]

The involvement of streptomycetes in MIC processes is not necessarily connected with their ability to form and develop biofilm; there are other mechanisms that are responsible for MIC.

3. Corrosive Activity of Streptomycetes

3.1. Production of Corrosive Compounds and Biodegradation of Corrosion Inhibitors by Streptomycetes

The production of corrosively active metabolites by micro-organisms is one of the mechanisms of their participation in MIC processes [17,50,51]. Streptomycetes are also producers of such compounds.

In particular, streptomycetes are well-known soil ammonifiers [52]. Researchers note that ammonifying bacteria participate in MIC at the beginning of biofilm formation and are able to form ammonia—a corrosively active metabolite [10]. In particular, the ammonifying ability was noted for streptomycetes *Streptomyces gardneri* (*S. gardneri*) strain ChNPU F3 and *Streptomyces canus* (*S. canus*) strain NUChC F2 isolated from soil that was in contact with the corroding steel fence post (the ferrosphere) [53,54].

Streptomyces are sulfur-oxidizing bacteria and are able to oxidize sulfur compounds [18]. *Streptomyces* sp. possessing such properties were isolated from the concrete structures of the bridge [55]. Bacteria produced H_2SO_4 and decreased culture pH up to 3.5. From the authors' point of view, this could cause the biodamage of construction materials. This strain was used in the study to simulate the microbial corrosion of concrete samples (which were then analyzed by FTIR) by biogenic sulfuric acid [56]. Wang et al. [57] showed that organic acids produced by *Streptomyces* sp. accelerated the corrosion damage of steel in the initial stages of MIC.

Streptomyces could be applied in the field of bioremediation as, in particular, they are capable of biotransformation and biodegradation [15]. In particular, there are reports of the utilization and transformation of *Streptomyces* sp. corrosion inhibitor benzimidazole as an energy source for these, and bacterial growth (using SEM analysis) on the mild steel samples coated with benzimidazole [58]. The authors emphasize the need to develop eco-friendly approaches—"green" biocides or biocides based on micro-organisms, and their analogues, which are incorporated into pre-existing benzimidazole to increase the level of corrosion inhibition against corrosion biofilms in conditions under the influence of actinobacteria.

3.2. The Intensification of Corrosion in Mixed Corrosive Microbial Associations with Strepomyces spp.

A decrease in the impedance value of A3 steel and an increase in the corrosion of steel were detected if streptomycetes grew together with *Nocardia* sp. [59]. In mono and associated bacterial systems (*Thiobacillus ferrooxidans* (*T. ferrooxidans*), *Streptomyces*, and *T. ferrooxidans* + *Streptomyces*), corrosion characteristics of A3 steel were investigated using electrochemical measurements and surface analysis. Serious damage to A3 steel was established with the participation of streptomycetes [60]. However, the MIC of steel was lower with the association of streptomycetes and *T. ferrooxidans*.

From an Indian crude oil reservoir, *S. parvus* strain B7 and *Bacillus subtilis* (*B. subtilis*) strain A1 were isolated. These strains in monocultures and associations were investigated as corrosion agents of carbon steel and stainless steel (API 5LX and 316, respectively) with the presence of an eco-friendly corrosion biocide/inhibitor [41]. The authors noted severe corrosion of both metals both by individual strains A1 and B7 and by association. It was noted that the association had the highest corrosion activity among the tested variants and *S. parvus* strain B7 showed higher corrosion activity than *B. subtilis* strain A1. The researchers decided that the corrosion activity of the studied microorganisms was related to the formation of biofilms (the presence of a "green" inhibitor inhibited this process) and the influence on the electrochemical parameters of the corrosion process.

In general, the corrosive activity of streptomycetes in monocultures and as part of associations is presented in Table 2.

Table 2. Corrosive activity of streptomycetes.

Cause of Corrosion Activity	Species (Compound)	Researched Construction Material	References
Powerful biofilm	*S. parvus* strain B7	carbon steel, stainless steel	[41]
Poor biofilm	*S. lividans* strains TK23.1 and TK24	SAE 1018 steel	[44,45]
	S. pilosus strain DSM40714	mild steel 37/AISI 10-18	[42]
Changes in electrochemical parameters	*Streptomyces* sp.	steel A3	[60]
Production of corrosive compounds	*S. gardneri* strain ChNPU F3, *S. canus* strain NUChC F2 (ammonia)	steel	[53]
	Streptomyces sp. (sulfuric acid)	concrete	[55,56]
	Streptomyces sp. (organic acids)	X65 steel	[57]
Biodegradation of corrosion inhibitors	*Streptomyces* sp.	benzimidazole-coated mild steel	[58]

4. The Prevention of Corrosion and Biofouling by *Streptomyces* spp.

4.1. Antimicrobial Metabolites of Streptomycetes in the Biocontrol of MIC

In recent years, the number of publications on "green" biocides/inhibitors, including the prevention of MIC processes, has been rapidly increasing [2,4,5,61]. Among such eco-friendly agents, considerable attention is paid to secondary metabolites synthesized by heterotrophic bacteria [4,43,62–64]. Streptomycetes are known as producers of a number of antimicrobial compounds [65]. Therefore, unique antibacterial metabolites of streptomycetes (antibiotics, lipopeptides, exopolysaccharides, and siderophores) are proposed as the agents of microbial control and prospective MIC inhibitors [48,57,66,67].

Thus, the ability to inhibit Zn corrosion in H_2SO_4 using albomycin synthesized by *Streptomyces griseus* (*S. griseus*) was defined [62]. There is a report on the reduction in corrosion losses of steel panels when using the strain *Streptomyces* sp. as a monoculture [24]. This strain was isolated from the Antarctic soil. A eumelanin polymer purified from *S. parvus* strain BSB49 has anticorrosive properties on mild steel samples [25]. The known classes of corrosion inhibitors, which are metabolites of various species of *Streptomyces*, are as follows: tetracyclines, macrolides, lincosamides (lincomycin), and aminoglycosides (streptomycin) [23].

It was found that *Streptomyces lunalinharesii* (*S. lunalinharesii*) strain 235 inhibits the growth of *Desulfovibrio alaskensis* strain NCIMB 13491 and *Bacillus pumilus* strain LF-4, which are participants in biofilm formation and the process of biocorrosion [68]. The prevention of SRB biofilm formation by this strain is due to antimicrobial substances that a strain forms [69]. It was noted that streptomycetes, producing a number of polysaccharides and acetylated amino acids, are able to inhibit corrosion processes in the middle stages (time) [57]. At the same time, the authors note the importance of the stability of the film layer for the inhibition process and the importance of using the antimicrobial metabolites of streptomycetes in MIC biocontrol. Polysaccharides belong to the group of biosurfactants [70], which deserve attention as bioactive, anticorrosive, and antibiofilm compounds [63,71]. Representatives of actinobacteria are known as producers of biosurfactants [72] and therefore, their participation in microbial corrosion processes is important.

The researchers evaluated the ability to inhibit the corrosion of SAE 1018 steel by both an intact non-viable biofilm (the cells of which were killed by the addition of kanamycin) and metabolites of the non-biofilm-forming strain *S. lividans* TK 24. The ability of the formed biofilm to inhibit corrosion under gentle agitation was also investigated [44].

Members of the genus *Streptomyces* are known to produce effective antifouling compounds [73]. The most active strains and their antibiofouling substances were as follows: *Streptomyces fungicidicus* (*S. fungicidicus*) (diketopiperazines) [74], *Streptomyces albidoflavus* (*S. albidoflavus*) strain UST040711-291 (a group of simple butenolides) [75], and *Streptomyces filamentosus* (*S. filamentosus*) strain R1 (according to the authors' assumption, requinomycin (antibiotic of the anthracycline group) [76]. Anticorrosive properties of the marine strain *Streptomyces* sp. were shown under MIC conditions induced by sulfate-reducing bacteria on X65 steel [77]. The researchers note that the strain grew by competing with SRB, reducing the rate of electrochemical reactions, and its metabolites inhibited SRB biofilm formation, which overall resulted in the inhibition of corrosion rates [77].

4.2. Nanoparticles and Streptomyces spp. as a Prospect of MIC Biocontrol

Today, researchers of corrosion processes give considerable attention to the use of nanoparticles in inhibitory protection [66,78].

Agarwal et al. [79] investigated its use against bacterial biofouling and steel corrosion (under salt water and acid conditions), using a combination of an extract of marine actinobacteria *Streptomyces* sp. strain VITDSB and its mediated zirconium oxide nanoparticles. The researchers recorded the highest effect against *Bacillus thuringiensis* and *Pseudomonas aeruginosa*, as well as an increased anticorrosion effect under the influence of both salt water and acid.

There are reports of formation by streptomycetes of metal nanoparticles and metal oxides nanoparticles [80–86]. The antimicrobial, antibiofilm/antibiofouling properties of both metal nanoparticles and metal oxides are being actively researched [87–91], as well as their inhibitory activity [66]. However, there are currently no studies on MIC processes in the presence of nanoparticles synthesized by streptomycetes. Currently, some species of bacteria, known as model organisms in MIC research processes, have shown sensitivity to silver nanoparticles biosynthesized by *Streptomyces naganishii* (*S. naganishii*) strain MA7 [87]. In particular, the silver nanoparticles showed antimicrobial properties against *Bacillus cereus, Escherichia coli, Staphylococcus aureus*, *Proteus mirabilis*, and *Pseudomonas aeruginosa*; antifouling properties were noted against *Aeromonas* sp. strain P26, *Aeromonas* sp. strain PP6, *Alcaligenes* sp. strain P47, *Alcaligenes* sp. strain PP8, *Bacillus* sp. strain P31, *Bacillus* sp. strain P46, *Micrococcus* sp. strain P56, *Micrococcus* sp. strain PP5, *Pseudomonas* sp. strain P1, and *Staphylococcus* sp. strain PP3 [87].

In general, the anticorrosion/antibiofouling activity of streptomycetes is presented in Table 3. Thus, in the biodamage of structural materials, streptomycetes play a dual role: either as corrosion enhancers or as corrosion inhibitors, which is determined by the specifics of the physiology of a certain strain and species.

Table 3. Anticorrosion and antibiofouling activity of streptomycetes.

Protective Activity	Species (Compound)	Researched Construction Material	References
Anticorrosion and/or antimicrobial/ antibiofouling compounds	*S. griseus* (albomycin)	zinc	[62]
	Streptomyces sp.	steel	[24]
	Streptomyces sp. (amino acids: phenylalanine, proline; polysaccharides)	X65 steel	[57]
	Streptomyces sp.	X65 steel	[77]
	S. parvus strain BSB49 (eumelanin)	mild steel	[25]
	S. fungicidicus (diketopiperazines)	not used (methods without the use of construction materials)	[71]
	S. albidoflavus strain UST040711-291 (a group of simple butenolides)	polyvinyl chloride	[72]
	S. filamentosus strain R1 (requinomycin)	the glass slides	[73]
	Streptomyces sp. strain VITSDSB (the combination of cultural extract and zirconium oxide nanoparticles)	steel	[74]
	Streptomyces sp. (tetracyclines, macrolides, lincosamides, aminoglycosides)	not specified	[23]
	S. lunalinharesii strain 235	not used (methods without the use of construction materials)	[68,69]
	S. naganishii strain MA7 (silver nanoparticles)	not specified	[87]

5. The Challenges and Potential Directions for Future Research

The involvement of streptomycetes in MIC processes has recently been actively studied. Streptomycetes are now known to either be corrosive agents in MIC or producers of compounds with anticorrosion properties (“green” inhibitors) that act as biological control compounds to protect materials from deterioration. The participation of streptomycetes in MIC processes is related to both the corrosive metabolites they produce and bioelectrochemical mechanisms. Antibiotics, pigments, amino acids, polysaccharides, and oxide nanoparticles produced by streptomycetes are important in terms of biodeterioration control approaches. Such compounds are eco-friendly and are considered promising “green” corrosion biocides/inhibitors.

At the same time, despite the success in inhibiting MIC using micro-organisms in laboratory conditions, such MIC inhibition methods have not achieved practical application and success [51]. Usually, such studies are short term, carried out in controlled laboratory conditions (which differ from the conditions of material exploitation in the environment). Also, biologically active compounds of micro-organisms can be involved in the circulation of substances, which will reduce their effectiveness. The preservation of producer strains requires considerable effort to prevent the loss of their biological activity. The process of identifying and isolating a biologically active compound with the properties of a MIC biocide/inhibitor appears to be expensive and labor-intensive. Therefore, the use of biological controls in the prevention of MIC requires further in-depth studies on the mechanisms of MIC, in particular regarding antagonistic interactions and the production of antimicrobial compounds by participants in the corrosion process. The use of biological controls should be considered as an eco-friendly alternative to chemical biocides/inhibitors for systems where temperature and humidity conditions can be controlled and the anticorrosion agent can be changed/added. In particular, this is useful for the prevention of biodeterioration in historical heritage sites [92]. Indeed, there are limitations to the practical use of streptomycete secondary metabolites for MIC prevention, but such compounds belong to the category of renewable resources and represent a completely new opportunity for the circular economy, which determines the need for further in-depth research [93].

Future research in this field should be directed toward the study of secondary metabolites and biosynthesized nanoparticles of metals and metal oxides with antimicrobial activity as "green" microbial corrosion inhibitors, as these compounds have been shown to have both antimicrobial and inhibitory properties. In addition, an important component of future research should be the study of the influence of streptomycetes, as producers of such compounds, on the structure of corrosion-active groups of micro-organisms. Thus, the mechanisms of involvement of *Streptomyces* spp. in the processes of the biodeterioration of some structural materials can be presented in the form of a general scheme (Figure 1).

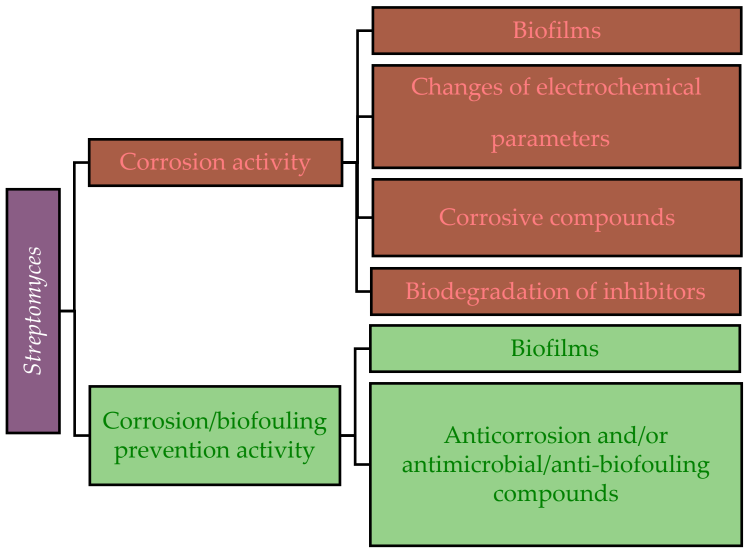

Figure 1. Mechanisms of participation of streptomycetes in biodeterioration of structural materials.

6. Conclusions

The results of research in the field of MIC and, in particular, the participation of streptomycetes in the corrosion process and the possible mechanisms of their involvement were summarized in the presented study. It was shown that representatives of the genus *Streptomyces* can affect the process of biodamage to structural materials in the following ways: 1. by biofilm formation; 2. by influencing the electrochemical characteristics of the corrosion process; 3. by participating in the biodegradation of corrosion inhibitors; and 4. by the production of anticorrosive/antimicrobial and/or corrosion-hazardous substances. At the same time, the mechanisms of streptomycetes' involvement in the processes of microbial damage to metals and their consequences (intensification or weakening of corrosion) are ambiguous and are determined by the peculiarities of the physiology of the studied species or strains and the presence of micro-organisms of other species. Further studies on streptomycetes as participants in the corrosion process with special attention to their production of secondary metabolites and nanoparticles with antimicrobial and inhibitory properties are necessary, which will contribute to the expansion of the list of "green" biocides/inhibitors.

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