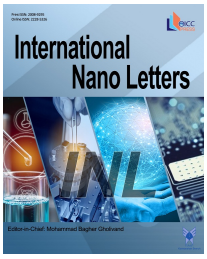

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Insight Mechanistic of Metal Nanoparticle-Microbe Interactions: A Review

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Abstract:

The modern era has accepted the significance of nanomaterials and their exploitation for the advancement of several disciplines. In view of the increasing applications and demand of nanomaterials, numerous techniques for the synthesis of nanoparticles (NPs) mediated by several means have been discovered, synthesis mediated by microorganisms being one of the most feasible ones. NPs have emerged as efficient drug carriers and as potential antimicrobials against existing diseases as a result of their interactions with microorganisms. The antimicrobial effect of biosynthetic NPs is contributed by the action of reactive oxygen species augmented by the capping agents that get adhered to the surface of NPs during the biosynthesis process. The present review discusses the use of various microorganisms for the biosynthesis of metal NPs through varied mechanisms that take place when microbes interact with aqueous solutions of metals. Furthermore, it aims to address the mechanistic insight into the metal nanoparticle-microbe interactions as potential antimicrobials. At the same time, it demonstrates the necessity of adopting a multidisciplinary approach for the exploitation of microbe-nanoparticle interactions in diverse plant species against a plethora of microbes affecting them.

Keywords: Metal NPs; Microbial biosynthesis; Metal-based therapeutic agents; Metal NP-Microbe interactions; Phytopathogens; Antimicrobial activity; Antibacterial activity; Antifungal activity; Antiviral activity

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1. Introduction

Nanotechnology, focusing on the synthesis and application of nanomaterials, is a rapidly advancing field in scientific research. Various methods for nanoparticle synthesis have been developed, with microorganism-mediated synthesis being highly effective [1, 2]. However, commercial scalability and molecular mechanisms require further exploration. Green synthesis of nanoparticles refers to using environmentally friendly and sustainable methods to produce nanoparticles, typically relying on biological sources and minimizing the use of toxic chemicals [3]. Microorganisms such as bacteria, algae, fungi, and yeasts can produce NPs by reducing metal ions [4]. Silver and gold nanoparticles (NPs), valued for their biocompatibility and low reactivity, are widely studied for applications in drug delivery and biosensors [5]. Biosynthetic NPs owe their stability to biomolecular capping agents from microorganisms, enhancing their compatibility with biological systems [6]. Research highlights their potent antimicrobial properties, offering potential treatments for infectious diseases caused by bacteria, fungi, viruses, and parasites [7]. With rising drug resistance posing a global health challenge [8], metal NPs, due to their unique physicochemical properties and ability to interact with cellular biomolecules, present a promising solution [9].

To further improve their therapeutic efficacy and targeting precision, metal NPs can be conjugated with biological en-

tities such as ligands, enzymes, antibodies, and drugs that possess specific binding capabilities. This biofunctionalization enhances their selectivity toward diseased cells and strengthens their ability to deliver drugs directly to pathological sites [9]. Additionally, such conjugation shields the NPs from immune detection, thereby increasing their stability and prolonging circulation within the bloodstream. Their unique surface charges and stability properties further contribute to their promise as antimicrobial agents. However, for successful biomedical application, these NPs must meet essential criteria, including biocompatibility, selective targeting, resistance to aggregation, affordability, and minimal toxicity [10].

This review centres on the promising use of metal-based NPs in combating infectious diseases, with a particular focus on their antimicrobial properties and biological effectiveness. It also delves into the mechanisms by which these NPs interact with microbial cells, thereby exerting their therapeutic effects, especially in the context of plant pathogens.

2. Microbial biosynthesis of metal-based NPs

Microorganisms serve as eco-friendly and cost-effective nanofactories for synthesizing NPs, offering a sustainable alternative to energy-intensive and toxic chemical methods. Through reductase enzymes, microbes detoxify and reduce metal salts into NPs with uniform size distribution [11]. The process begins with preparing an aqueous metal salt solution, such as silver nitrate for silver NPs (AgNPs), $AuCl_4$ for gold NPs (AuNPs), or ferric chloride/ferrous sulfate for iron oxide NPs (IONPs). This solution is mixed with microbial culture, cell extract, or sterile filtrate in optimized ratios, leading to metal ion reduction and nanoparticle formation as depicted in Fig. 1. Extracellular synthesis is preferred over intracellular methods due to simpler recovery processes, eliminating steps like sonication, centrifugation, and extensive purification [12]. Biomolecules such as proteins, peptides, enzymes, and organic compounds act as reducing and capping agents, preventing aggregation and enhancing nanoparticle stability [13]. Bacteria have been successfully used to produce silver and gold NPs, with functional groups like alkaloids, phenolic compounds, and polyphenols aiding in reduction and stabilization [14]. Over the recent years, several microorganisms, including bacteria, fungi, and yeasts, have been studied extensively for the synthesis of metal NPs (Table 1).

3. Mechanism underlying microbial biosynthesis of metal-based NPs

Most of the studies on NPs involve the demonstration of nanoparticle biosynthesis processes, but very few illuminate the mechanism underlying the same, and that too by the postulation of expected mechanisms. The basic procedure involved in all these studies can be summarized in the form of the following steps: Firstly, the metal ions get concentrated on or within the cells of the microbes. Subsequently, the ions tend to undergo a reduction process, transitioning to their zero-valence state. This reduction process can lead to the formation of agglomerated structures, where individual atoms cluster together. As these clusters grow, they may aggregate into particles of nanoscale dimensions. These nano-sized particles can exhibit enhanced stability due to their reduced surface energy and cohesive forces between atoms, resulting in stable structures that resist further agglomeration. The reduction processes in the beginning are caused by the action of microbial enzymes or metabolites. In view of cell-free culture supernatant or a filtrate, direct reduction of the ions takes place by reducing agents as produced due to the microbial metabolism. Metals being a part of the environmental components can penetrate into cells further, causing disruption of the cell membrane structure, inactivation of cellular enzymes, and production of antimetabolites, which form a chelate with indispensable metabolites projecting to toxicity or cell death for the microbial cells [15, 16]. As such, microbes interact with the metals, resulting in either of the following: Metal elimination, transformation of their properties, or their accumulation away from key organelles. This mainly occurs as a stress response of the microbe to exhibit an adaptive or defense mechanism against metal toxicity. Thus, the microbes that can facilitate the synthesis of NPs are generally resistant to metals. For instance, bacteria genera like *Pseudomonas* can grow in high metal concentrations, as reported by Luo et al. (2015) [17]. The interaction of the anionic microbial cell components with the cationic metal ions may result in the generation of metal, metal oxide, or metal sulfide NPs via diverse processes like chelation, reduction, or hydrolysis [18]. The NP synthesis mechanism mainly involves either of the pathways involving proteins, enzymes, exo-polysaccharides, and electron shuttle quinones [19], which may often be mediated due to external parameters such as temperature and pH significantly influencing the NPs' properties such as size, concentration, etc. [20]. A few mechanisms that define the cause behind the microbial ability to synthesize NPs have been hypothesized. However, the understanding of the mechanism behind microbial synthesis of NPs remains largely speculative. Despite the progress in this field, several theories have been proposed to explain the potential mechanisms involved in microbial synthesis of NPs. Some of these include:

3.1 Ion reduction theory based on enzymatic action

Microbial enzymes are crucial for synthesizing NPs from metal ions through redox reactions, enabling nanoparticle formation either inside (intracellular) or outside (extracellular) the cell, with enzymes serving as nucleation sites [21]. In intracellular synthesis, metal ions bind to negatively charged cell wall groups, enter the cell, and are reduced by proteins and cofactors. Extracellular synthesis occurs in the surrounding medium, where secreted enzymes, proteins, or organic molecules reduce metal ions without cell entry [22, 23]. Microbes detoxify metals using enzymes like oxidoreductases and transporters, which convert toxic metal ions into stable NPs using electrons from cofactors like NADH [24–26]. For example, *E. coli* employs nitrate reductase to reduce selenate and tellurite ions while *Bacillus licheniformis* uses it to form silver NPs [27, 28]. Fungi like *Fusarium oxysporum* utilize high-molecular-weight proteins

and NADH-dependent reductases for silver nanoparticle synthesis [29]. In palladium nanoparticle production, hydrogenase enzymes in *Desulfovibrio fructosivorans* reduce Pd(II) ions [21, 30]. Fungal species like *Verticillium sp.* bind positively charged metal ions to carboxylate groups on their cell walls, triggering enzyme production to reduce ions into stable silver and gold NPs [31]. These studies underscore the pivotal role of enzymes, particularly NADH-dependent reductases and hydrogenases, in microbial nanoparticle synthesis.

Besides enzymes, microorganisms also secrete some other organic substances like enzymatic metabolites, non-catalytic proteins, and polysaccharides, which are thought to be reducing agents responsible for the formation of NPs. This fact can be supported by the study of Wei et al. (2012), in which culture filtrate of *B. amyloliquefaciens* was treated to deactivate the enzymes present in the filtrate [32]. Unexpectedly, the synthesis of AgNPs was still induced despite the addition of CFCF. This led to the suggestion that induction of AgNPs formation and stabilization was due to the functional groups provided by the bacterial proteins. Aforementioned, the proteins synthesized by the fungus *F. oxysporum*, induced the formation of AgNPs and provided resultant stability to the particles [33]. It has been proposed that the formation and stabilization of NPs can be credited to certain polysaccharides produced by cyanobacteria [29]. Conclusively, these studies reflect the fact that proteins, including the reduction-catalyzing enzymes produced by the microbes, significantly contribute to the reduction of metal ions into the NPs. Aldehyde-containing sugars act as reducing agents of the cell wall and may also be involved in these redox processes [19, 34]. Besides enzymes, other biological molecules like proteins, polysaccharides, and microbial cell wall secretions also play an important role in nanoparticle synthesis. Proteins, in particular, are known for their stabilizing properties [35]. For example, cysteine and amino groups in proteins can attach to the surface of gold NPs, helping to keep them stable. Tyrosine, under certain conditions, can bind to gold through its amine group and assist in reducing silver ions at high pH levels, which helps create gold core–silver shell structures [36]. Similarly, tryptophan can contribute to nanoparticle formation at basic pH by donating electrons through a temporary radical formed during its conversion in peptides [35]. These natural biological interactions not only support the synthesis of NPs but also enhance their durability and effectiveness. The synthesis mechanism of NPs being composed of three main phases, viz., activation, growth, and termination. In the context of metal biomineralization induced by fungi that involves electrostatic interaction of metal ions with the surface of fungal spores, some researchers have also named these steps "trapping" and "bioreduction" [37]. Therefore, a previous step of biosorption may also be included and imported for those systems where the subsequent steps tend to be intracellular. Accordingly, metal bioreduction is then accomplished by the enzymes that are present in the cell wall, followed by the aggregation of the reduced ions into small clusters, which can further coalesce into metal NPs, eventually attaining a stable shape and size of the formed NPs. These particles could then be further stabilized by an organic coating [38].

3.2 UV photo-conversion theory

As proposed by Wang et al. (2013), AgCl could form AgNPs by UV photo-conversion mediated by DNA templates. Rapid production of AgNPs is recorded due to the photosensitivity of AgCl [39]. Exploitation of such an effect may be accomplished by employing visible light irradiation, which may be enhanced by the specific dyes or color sensitizers. This theory can be stated as a photon from visible light is absorbed by AgCl crystals, which leads to the generation of an electron-hole pair, followed by a combination of e^- and Ag^+, which may further lead to the clustering of silver species in the presence of peptides or proteins. This photo-conversion of silver ion to Ag_0 can be accelerated by crucial proteins like metallothioneins that possess the abilities to bind silver species and scavenge superoxide and hydroxyl radicals [26].

3.3 Molecular mechanisms

Most of the literature employs AgNPs; hence, these are the commonly cited NPs in the field of nanotechnology [21, 40]. However, the metal ion reduction mechanism is similar to the AgNPs formation mechanism(s) in one or more steps for various NPs. It should be strictly mentioned that for silver, only 1 e^- reduction is required to obtain an atom, whereas for other metal ions like palladium, platinum, or gold, typically 2 or 3 electrons are needed to form the corresponding atom. Silver doesn't have any biological role in the body, & Ag_0 atoms are easily reoxidized. Due to this reason, there is a potential rate-limiting step in getting the threshold amount of silver atoms to coagulate for nucleation. Accordingly, further growth into silver NPs can occur as devised earlier [26, 40].

3.3.1 Molecular mechanism of biomineralization

Bacteria can turn metal ions into metal NPs through a process that starts with the transfer of electrons using natural reducing agents. Scientists have identified three main ways this happens:

a) **Extracellular Reduction (Outside the Cell):** In this method, metal ions are reduced outside the bacterial cell by substances found in the surrounding environment, such as nutrients, metabolites, or components in the culture medium. These substances, acting like natural reducing agents (similar to citric acid or ascorbic acid in lab-made reactions), help convert metal ions into their metallic form. Once the NPs start forming, biomolecules can stick to their surface. These molecules act as natural stabilizers called capping agents which keep the particles from clumping together and help control their size and shape [41–43].

b) **Light-Driven Reduction:** Here, light energy helps drive the process. When exposed to light, certain biomolecules or metal ions get excited and release electrons that reduce metal ions into NPs. Biomolecules like light-sensitive proteins or chromophores are involved in this electron transfer. As in the first method,

proteins and peptides act as capping agents to stabilize and shape the NPs during formation. This light-assisted method is often used in photobiosynthesis, allowing more control over how the NPs form [44].

c) **Cell-Surface-Mediated Reduction:** This approach happens directly on the surface of bacterial cells. Parts of the cell, such as the wall, pili, flagella, or membrane proteins, come into direct contact with metal ions. These biological structures act as natural catalysts, pulling electrons from the cell's metabolism to reduce the metal ions into NPs. Because the reduction takes place right on the cell surface, it creates a close, continuous interaction that supports efficient nanoparticle formation [34].

The processes discussed above can be supported with some of the research studies outlined here. Other than the aforementioned proteins, myriad proteins are the other biological entities believed to be responsible for microbial NP synthesis. Various transport proteins and peptides are engaged in the capping and stabilization mechanism of the created nano-metallic structures and intracellular entry of metals [45]. Especially in the case of magnetic NPs, magnetosome membrane proteins are employed by MTB for biomineralization. Another study demonstrated the isolation of a minute acidic protein, Mms6, and its utilization to precipitate uniform cobalt ferrite nanocrystals [30]. Another study demonstrated the accumulation of CdS NPs by yeast strains of *Schizosaccharomyces pombe* and *Candida glabrata* inside the cell plasma coated with phytochelatins, which is a peptide known to prohibit DNA disruption and cell cycle damage occurring due to metal toxicity [38].

3.3.2 Efflux pump systems

These systems are vital in combating metal toxicity by removing toxic metal ions, preventing them from clustering around and entering microbial cells. A metal-resistant phenotype often carries efflux pump genes, such as those responsible for multidrug resistance (MDR), which can impact the organism's ability to synthesize nano-metals. The BaeSR system regulates RND (resistance, nodulation, and cell division) efflux pumps, aiding metal and antibiotic resistance by expelling ions and reducing porins in *E. coli* [46–48].

3.3.3 Interaction with organelles and biomolecules

A clear understanding of metal interactions with organelles and biomolecules is crucial for studying cell-metal interactions and nanoparticle synthesis. Liu et al. (2012) showed silver NPs forming via plasmid DNA ($\sim$ 4 kb) acting as a reducing agent through electrostatic complexation with Ag ions, enhanced by UV irradiation [49]. Ghosh et al. (2021) reported the porin docking from *M. smegmatis* onto self-assembled thiosulfates, leading to electrodeposition of proteins and copper NPs on gold [21]. Iravani and Verma (2019) supported their use in transistor applications [50]. Similarly, Hernandez-Garcia et al. (2012) synthesized protein nanostructures via genetically engineered *Pichia pastoris* for DNA coating in gene delivery [51].

3.3.4 Genetics-associated molecular mechanisms for metal nanotization

Expression of particular heavy metal resistance genes (MRGs) is one of the mechanisms by which bacteria respond so as to escape the toxicity caused by elevated concentrations of heavy metals. These genes can be easily transferred to the neighbouring microbial communities due to their common presence in plasmids or transposons and have been studied extensively for the elucidation of the mechanisms underlying nanotization. Roosa et al. (2014) used qPCR to assess metal availability and showed czcA aids Cd/Zn/Co efflux in microbes [52]. Chen et al. (2019) identified various metal resistance genes—including arsB/C (arsenic), copA/B and pcoA-D (copper), czcA/C/D, nccA (nickel), pbrT (lead), and chrB (chromium)-at a copper tailing site in China [53]. Randall et al. (2015) reported the sil operon, with silG, involved in silver resistance [54]. High levels of efflux systems like RND transporters, P-type ATPases, and OMF/MFP complexes combat metal toxicity. Saravanan et al. (2022) highlighted genetically engineered microbes (GEMs) using these genes for nanoparticle synthesis and bioremediation [55]. Ghosh et al. (2021), observed phytochelatin synthetase from *S. pombe* stabilizing CdS nanocrystals via nucleation, preventing aggregation [21].

4. Applications of metal-based NPs as therapeutic agents

Over the years, numerous studies have emphasized the potential applications of NPs in biomedicine and agriculture (Fig. 2), showcasing their versatility across these fields [56–58]. Researchers have increasingly explored the unique properties of metal-based NPs, applying them in areas such as targeted drug delivery, gene therapy, DNA analysis, biosensing, cancer treatment, antibacterial agents, and the enhancement of reaction rates. These diverse applications underscore the transformative role of NPs in advancing medical and agricultural innovations. Below are some examples that illustrate these cutting-edge applications [59].

4.1 Drug delivery:

NPs enable precise drug delivery by penetrating biological barriers like the blood-brain barrier, improving drug bioavailability and reducing side effects through enhanced pharmacokinetics [60]. They enhance solubility of hydrophobic drugs and stabilize sensitive therapeutics [59]. AuNPs are valued for biocompatibility, though biosynthesized versions need more exploration [61]. The AgNPs offer antimicrobial and anti-inflammatory properties, with *Bacillus licheniformis*-synthesized AgNPs showing anti-angiogenic effects, despite toxicity concerns. Magnetic NPs (Fe_3O_4, Fe_2O_3) are promising for targeted therapies like hyperthermia and diagnostics [62].

4.2 Antimicrobial agents:

Metal NPs combat antibiotic resistance effectively. *Trichoderma viride*-synthesized AgNPs (5-40 nm) enhance antibiotics like ampicillin against bacteria [63]. AuNPs show antimicrobial activity against pathogens and inhibit early HIV replication when combined with azidothymidine

[64, 65]. Light-enhanced anti-leishmanial effects are reported for NPs [66]. Copper NPs (CuNPs) are cost-effective antifungals for plant diseases [67–71].

4.3 Biosensors:

NPs enhance biosensor performance due to their unique properties. *Bacillus subtilis*-produced selenium NPs (50-400 nm) enable sensitive hydrogen peroxide detection for food, medical, and environmental applications [72, 73]. Yeast-derived gold-silver alloy NPs improve vanillin detection in tea and beans [74]. AuNPs enhance glucose oxidase activity for accurate glucose sensing in medical applications [75, 76].

4.4 Reaction-rate enhancement agent:

NPs have a large surface area and special traits that make them great for speeding up chemical reactions as catalysts or reducing agents [77]. Magnetic NPs are especially good at boosting reactions involving microbes. They spread well and have strong catalytic powers, making them perfect for many uses. For example, Shan and others used magnetic Fe_3O_4 NPs to coat *P. delafieldii* bacteria, helping remove sulfur from dibenzothiophene. These NPs stuck tightly to the bacteria due to their high surface energy. By applying a magnetic field, the bacteria spread evenly in the solution without needing extra mixing, and they could be easily collected and reused. The study showed that the bacteria's sulfur-removal ability stayed strong, and they could be reused multiple times without losing effectiveness [78].

4.5 Magnetic separation and detection:

Magnetic NPs conjugated with biomolecules enable sensitive detection in assays, such as chemiluminescence immunoassays using bacterial magnetic particles for detecting pollutants. Surface-modified magnetic NPs excel as adsorbents in DNA extraction, easily manipulated by magnetic fields, enhancing biomedical and environmental applications. These methods not only offer a lower detection limit but also provide a broader detection range compared to traditional ELISA techniques. One exciting area of research is the surface modification of magnetic NPs, which holds significant potential for various applications. Their use as solid-phase adsorbents, particularly in DNA extraction, is highly effective due to the ease with which these NPs can be manipulated using simple magnetic fields [79, 80]. This versatility in both detection and manipulation makes magnetic NPs a vital tool in biomedical and environmental research.

5. Applications of metal-based NPs as antimicrobial agents

NPs exhibit antimicrobial activity as a result of their ability to generate reactive oxygen species (ROS) that destroy the bacterial cellular organization and their affinity towards nucleic acids, namely DNA or RNA, thus hindering the replication processes (Fig. 3). Penetrations of the membrane boundaries are comparatively easier for NPs, as attributed to their small size. This helps them to get easily absorbed into the bloodstream [81]. Over the years, several research studies have demonstrated the biosynthesis of various metal-based NPs and assessment of their antimicrobial activities (Table 1 and Table 2). The toxicity mechanism of metal NPs on various microorganisms varies significantly. Antibacterial activity has been reported as a characteristic of several metal-based NPs [10].

5.1 Metal-based NPs as antimicrobial agents

Many studies have explored how metal NPs can fight infections by acting as antimicrobial agents (Table 2). Tiwari et al. (2011) tested AuNPs (combined with 5-fluorouracil) against bacteria and fungi [82]. They found these NPs worked better against Gram-negative bacteria, as they could easily enter those cells [83] used *A. niger* to prepare silver and zinc NPs, which showed antifungal effects against *Alternaria solani* (causing potato blight). Synthesis of 15 nm silver NPs using *Ganoderma enigmaticum* was reported, showing strong antibacterial effects against various bacteria [26]. Copper NPs were effective against various pathogenic bacteria [84]. Biologically prepared copper NPs also strongly reduced bacterial growth, creating prominent inhibition zones [85]. The effectiveness of metal NPs in eliminating pathogens stems from their small size and high surface-to-volume ratio, enabling strong interactions with bacterial membranes rather than just releasing metal ions into the solution (Fig. 4).

NPs demonstrate antifungal activity through multiple mechanisms, as illustrated in Fig. 5 [86]. They release ions that bind to protein groups, disrupting membrane protein function and altering cell permeability. Additionally, NPs inhibit fungal conidia germination, preventing growth, and interfere with biochemical pathways like electron transport and protein oxidation, which changes the fungal membrane potential. They also disrupt the protein oxidative electron transport chain, crucial for energy production, and increase oxidative stress (ROS)-related gene transcription, impairing mitochondrial membrane potential. Furthermore, ROS generated by NPs cause oxidative damage to proteins, membranes, and DNA, hindering nutrient uptake, while their ions induce genotoxic effects by damaging DNA, ultimately leading to cell death. This multi-faceted approach ensures a potent antifungal effect by targeting various cellular processes, rendering fungal cells dysfunctional.

Viruses, among the smallest and deadliest microorganisms, infect all living organisms, causing widespread diseases and mortality globally while persisting in various environments [87]. Although vaccines have eradicated diseases like smallpox, emerging viral pathogens, such as HIV and COVID-19, pose significant challenges due to limited treatment options, metallic NPs offer a promising solution as antiviral agents against these lethal viruses [88]. Research indicates that nanoparticle size significantly influences their antiviral efficacy by enabling direct interaction with viral genomes and surface proteins [87]. Their small size enhances penetration into the viral genome, potentially disrupting replication by blocking cellular and viral factors (Fig. 6). In the context of agriculture, silver NPs are the most commonly investigated NPs, which can be used as antiviral agents [89, 90]. Viruses, due to their evolving and fatal nature, cause numerous plant diseases, which tend to be typical to manage; sometimes

they are almost incurable. Therefore, viral infections require appropriate and effective management ideas. As is evident from the present literature, the viral multiplication cycle includes the following main steps: (i) Replication of virus in the cells, (ii) Biosynthesis of genome and viral components, (iii) Assembly of viral components, and (iv) Emission of viral particles from its host cell [91]. The Ag-NPs can fight viruses by binding to gp120, blocking virus attachment to cells, destroying viral particles before they enter, and interacting with viral DNA [87]. Studies show silver NPs also interact with the protein coats of potato virus Y (PVY) and tomato mosaic virus (ToMV) [92, 93]. They can directly break down Tobacco Mosaic Virus (TMV) by damaging its shell proteins and causing them to clump and fall apart. Elbeshehy et al. (2015) found that silver NPs made by *Bacillus sp.* had harmful effects on YBMV [94].

6. Metal nanoparticle-microbe interactions: Possible mechanisms responsible for the antimicrobial behavior of NPs

6.1 Decomposition of NPs into metal ions

Lewis acid-base reactions help free metal ions contribute to the antimicrobial action of NPs. In cells, sulfides and phosphates act as Lewis bases, while silver acts as a Lewis acid. When soft acids and soft bases react, like silver with important cell proteins, it can inactivate the proteins and kill the cell [26]. The reverting back of NPs to their predecessor or ionic form occurs while they are acting on microorganisms [95]. This can further allow all the chemical changes specific to metal ions to occur, which get potentially enhanced as a result of high (localized) ion concentration due to the delivery of NPs. Feng et al., in a study, stated that the decomposition of silver NPs into silver ions was the reason behind the antimicrobial activity against the bacterial cells [96]. However, this process of conversion into ionic form to produce an antimicrobial effect also depends on the medium, as is evident from several research studies [97]. The entrance of these silver ions into the cells leads to the cell's destruction and inhibition of its vital functions. Additionally, these silver ions may also induce other abnormalities like inhibition of respiratory enzymes, inactivation of -SH groups of bacterial enzymes, and interaction with proteins. They may further get involved in the replacement of protons in the hydrogen bonds of DNA, which hold its double-helical structure together.

6.2 Generation of ROS

Exposure of silver ions to cells can lead to the generation of ROS as a result of the disruption of iron sulfide clusters present in respiratory enzymes, which subsequently releases the iron atom that can further catalyze Fenton reactions. However, this mechanism, including Fenton reactions and subsequent Haber-Weiss reactions, could not be observed in every case for all the metal NPs [26]. Some transition metal NPs can cause the production of ROS inside cells, which can be very harmful [98]. Light can activate titanium oxide and zinc oxide NPs, leading to ROS generation. Negatively charged ROS usually stay outside the cell, but positively charged ones, like protonated hydrogen peroxide, can enter and damage cells. A recent study showed that ZnO NPs create ROS in *C. jejuni*, but Zn^{2+} ions alone do not cause ROS inside cells [26].

6.3 Effect on specific cellular process

6.3.1 Derangement of integrity of cell membrane

Due to high penetration power, silver NPs may creep into the cell wall of the bacteria by disrupting its structural organization. This involves adhesion of particles to the surface, thus causing distortions on the cell membrane, which may subsequently affect membrane permeability in a significant manner, resulting in cell death. Formation of such aberrations in proximity to each other may lead to the formation of micro pits on the cell surface in which NPs may subsequently get assembled. Some studies on electron spin resonance spectroscopy have reported the formation of such aberrations on the bacterial cell wall due to the generation of ROS caused by silver NPs [99]. However, the specificity of this effect to the NPs or from the locally released silver ions is yet to be investigated and defined.

6.3.2 Disturbance in signal transduction

NPs, when exposed to bacterial cells, are likely to interfere in their signal transduction mechanism [100]. Phosphorylation of proteins is one of the major factors in the signal transduction process. Shrivastava et al. (2007) reported that exposure of the Gram-negative bacterial cells to the silver NPs resulted in dephosphorylation on the tyrosine residues, leading to disturbance in signal transduction and subsequent inhibition of growth of the bacterial cell [101]. Further study and investigation on overall signalling processes in response to NPs is a major requisite.

6.3.3 Chemotaxis and cell motility

Chemotaxis is how bacteria move in response to chemical changes, controlled by specific genes and signaling across the cell. Genes like *tar*, *str*, and *tap* encode sensory receptors, while *fli* genes control flagella production, and *che* and *mot* genes handle movement signalling [102]. AuNPs were found to affect bacterial chemotaxis and motility in a swarm plate test. At first, *E. coli* grew large swarm colonies within four hours when treated with AuNPs. However, after longer exposure (eight to twenty hours), their movement slowed, and higher NP concentrations gradually reduced colony size, likely due to energy exhaustion [103].

7. Conclusions and future prospects

In recent years, many studies have shown that metal NPs have strong antimicrobial properties. Their unique characteristics make them especially effective against microbial plant pathogens. However, despite strong evidence supporting the use of metal NPs in creating antimicrobial agents, there are growing concerns about their environmental impact, especially the risk of plants absorbing too much of these particles. Therefore, more research is needed to ensure their safe and responsible use. Recently, innovative approaches such as using magnetic and surface-functionalized NPs have been proposed to better control their release, maintain antimicrobial activity, and reduce the risk of environ-

mental contamination. Even so, this field offers many opportunities for further research and improvement.
Although several mechanisms for biogenic nanoparticle synthesis have been suggested, there is an urgent need for deeper studies to better understand the role of reducing enzymes, catalytic proteins, and stabilizing agents. This knowledge is essential for improving microbial modifications and engineering their metabolic pathways. Only with a clear understanding can real progress be made in biogenic synthesis. Metal NPs offer exciting new strategies to fight plant diseases compared to traditional treatments. Silver NPs have been widely tested, but they can be toxic to plants and beneficial microbes. Therefore, metals like iron, zinc, magnesium, and manganese, which are less toxic, should also be studied. It is important to determine the minimum inhibitory concentration (MIC) of metal NPs both in the lab (*in vitro*) and in real plant systems (*in vivo*). Special attention must be given to the toxicity of NPs to ensure they harm pathogens more than helpful microbes. Research must also explore how NPs affect plants and soil microbiota. Overall, this field holds great promise for developing safe, effective therapies by combining knowledge from multiple scientific areas. At the same time, urgent efforts are needed to create treatments against microbes that are resistant to current antimicrobial agents.

Authors Contribution
AS: Led the literature search, and drafted the initial version of the manuscript. NB: Contributed to data collection, literature review, and writing sections related to the biological implications of metal NPs. SS: Assisted in data collection and organization. SSG: Provided critical revisions and insights on the mechanistic aspects of nanoparticle–microbe interactions and assisted in organizing the structure of the review. DP: Contributed to editing and refining the manuscript, and provided feedback on the ecological and environmental impacts of nanoparticle interactions. GS: Conceptualized the review, coordinated among authors, and contributed to the final revision of the manuscript.

Availability of data and materials
The data that support the findings of this study are available from the corresponding author, upon reasonable request.

Conflict of interests
The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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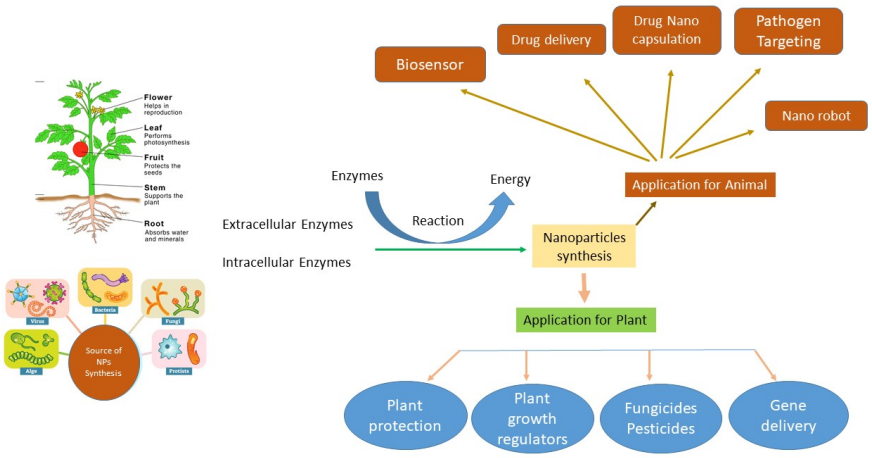

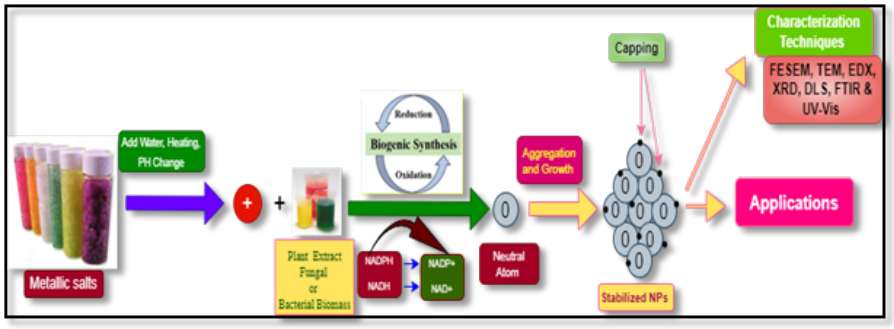

Figure 1. Mechanism of synthesis of metal NPs by microbial and plant extract. The general mechanism includes reduction of metal ions by phytochemicals or reductase enzymes present in the microbial extract to ultimately produce metal NPs. The biomolecules provide natural capping to NPs. The synthesized NPs can be characterized in terms of their size, shape, or concentration by various physical techniques (FESEM, TEM, EDX, XRD, DLS, FTIR, UV-Vis Spectrophotometer, etc.) and used for their potential application in different fields.

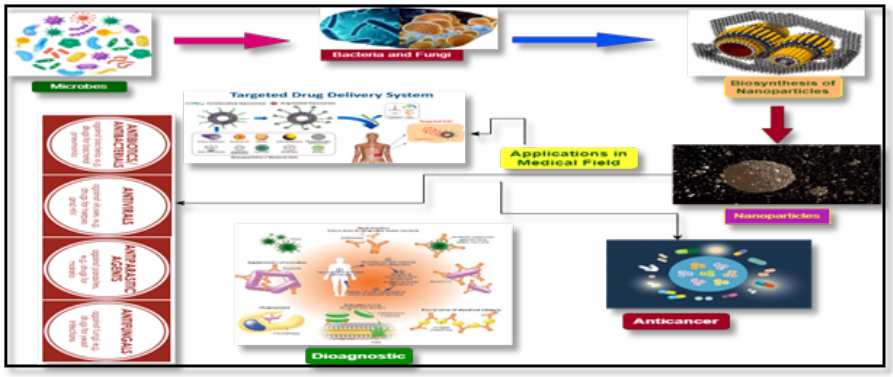

Figure 2. Microbial Biosynthesis of NPs and their potential applications as therapeutic agents.

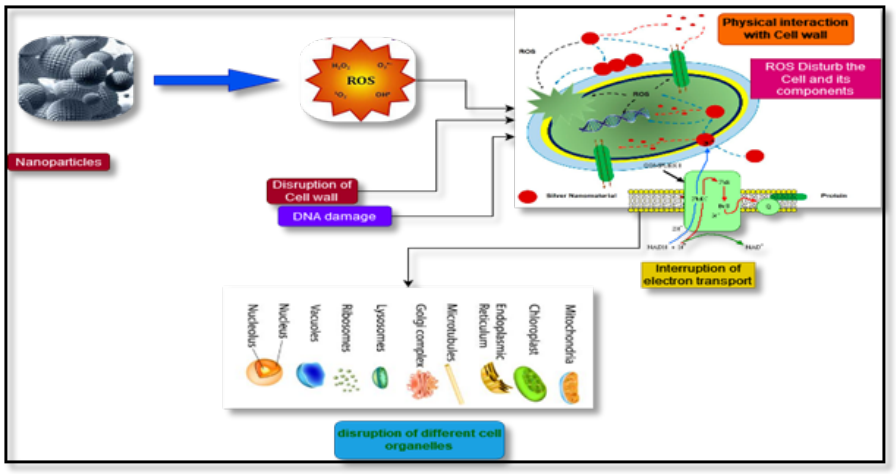

Figure 3. Mechanisms of antimicrobial activity of the metal NPs. The NPs can easily penetrate the microbial cell wall due to their fine size, where they stimulate the release of ROS that ultimately disturb the electron transport across the membrane and destroy the cell.

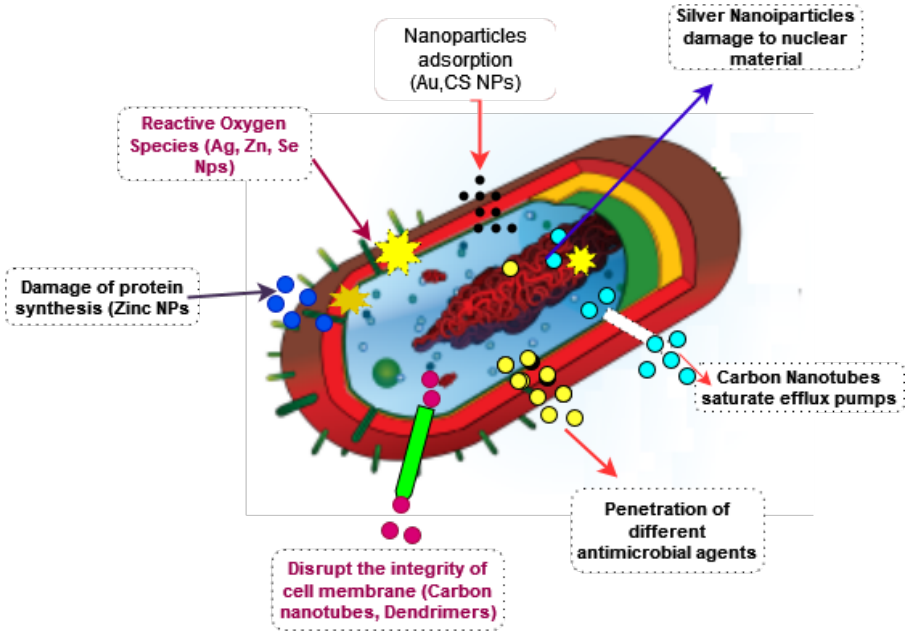

Figure 4. Illustration of the possible mechanisms of action of metal NPs on pathogenic bacteria.

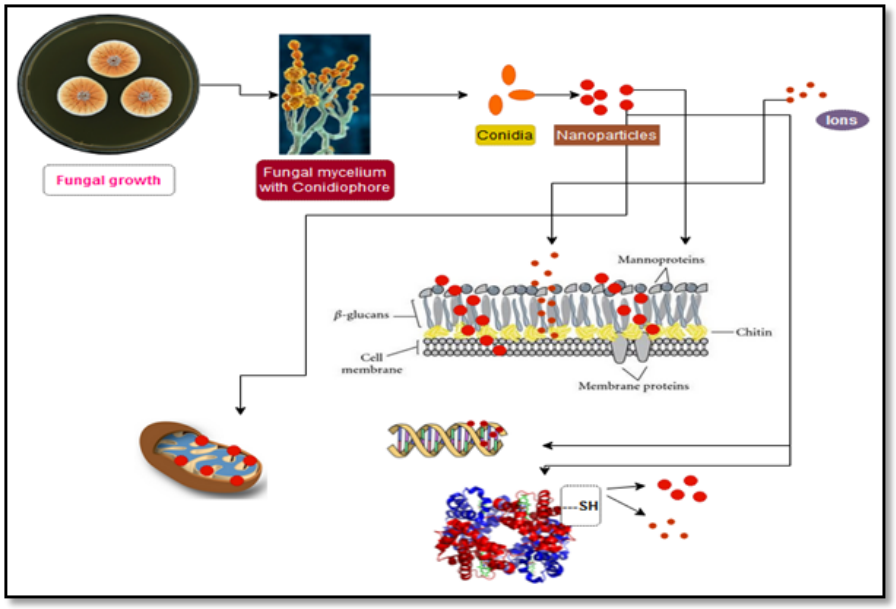

Figure 5. Illustration of the possible mechanisms of action of metal NPs on pathogenic fungi. The NPs cross the fungal cell wall and disrupt the ion channels of various cell organelles, disturbing the ion influx and causing the liberation of ROS. The ROS damages different components of the cell, including nucleic acids, which ultimately kills the fungi.

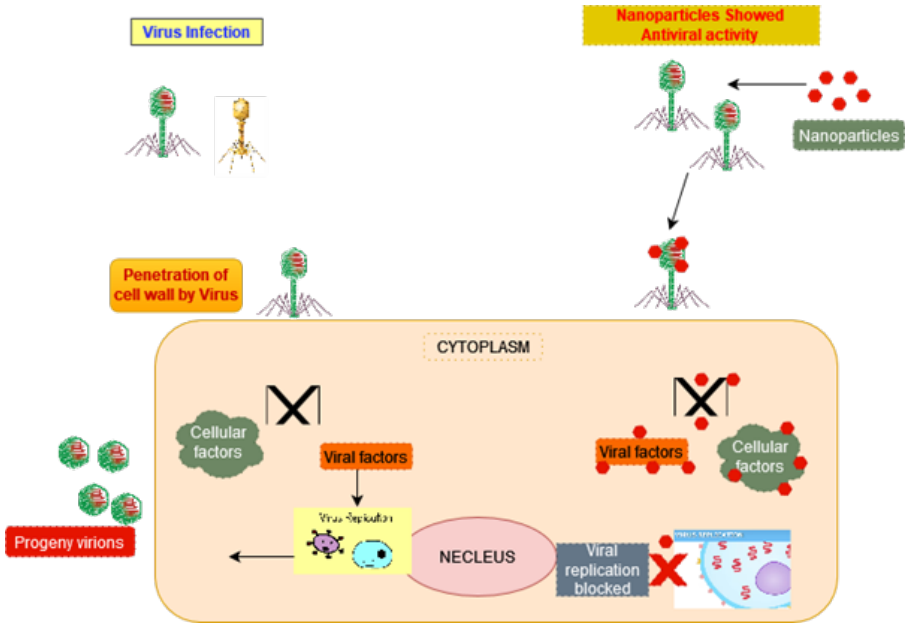

Figure 6. The NPs can either bind with the viral particles outside the cell surface or viral nucleic acid inside the cell. The binding of NPs with the viral components hinders the infection efficacy of the viruses.

Table 1. Metal NPs synthesized by various microorganisms.

Microbes used for synthesis	Metal Nanoparticle	Size (nm)	Shape	References
Fungi (mold)				
Trichoderma sp.	Iron	-	-	[104]
Fusarium oxysporum	Platinum	25	Cubical, spherical and truncated triangular	[105]
Colleotrichum sp.	Aluminium	39	Cubic	[106]
Aspergillus oryzae	Silver	∼110	Spherical	[107]
Rhizoctonia solani	Silver	10-20	Crystallite	[108]
Aspergillus niger	Zinc	76.2-183.8	Spherical	[109]
Neurospora crassa	Silver, gold, bimetallic silver and gold	>100	Quasi-spherical	[110]
Rhizopus orizae	Magnesium	∼ 20	Spherical	[111]
Trametes trogii	Silver	5-65	Spherical- Ellipsoidal	[112]
Aspergillus flavus	Silver	35	Spherical	[113]
Bacteria				
Shewanella oneidensis	Copper	20–40	Spherical	[114]
Bacillus amyloliquefaciens	Silver	5–40	Spherical	[115]
Brevibacterium casei	Gold	9.5-52.3	Spherical and triangle	[116]
Bacillus methylotrophicus	Silver	10-30	Spherical	[117]
Enterobacter cloacae	Silver	15-44	Spherical	[118]
Weissella oryzae	Zinc	∼8	Spherical	[119]
Bacillus cereus	Silver	3-20	Spherical	[120]
Pseudomonas putida	Zinc	25–45	Spherical	[121]
Algae				
Caulerpa racemosa	Gold	13-85	Spherical-oval	[122]
Turbinaria conoides	Iron	∼28	Spherical	[123]
Sargassum tenerrimum	Silver	13-46	Spherical	[124]
Cystoseira baccata and *C. tamariscifolia*	Silver	22	Spherical	[125]
Caulerpa sertularioides	Zinc	<100	Spherical	[126]
Fungi (yeast)				
Yarrowia lipolytica	Silver	∼16	Spherical	[127]
Candida parapsilosis	Silver	∼25	Spherical	[128]
Extremophilic yeast	Silver and gold	Silver-20; gold-30–100	Irregular	[129]

Table 2. Metal NPs as Antimicrobial agents.

Name of the Microbe used for NPs' synthesis	Metal NPs	Antimicrobial activity	Activity against pathogen	References
Bacteria				
Pseudomonas rhodesiae	Silver	Antibacterial	*Dickeya dadantii*	[130]
P. putida	Zinc	Antibacterial	*E. coli*, *E. faecalis*	[121]
Bacillus siamensis	Silver	Antibacterial	*Xanthomonas oryzae pv. Oryzae*	[131]
Bacillus cereus	Silver	Antibacterial	*X. oryzae pv. Oryzae*	[132]
Bacillus megaterium	Iron	Antibacterial	*Staphylococcus aureus*, *B. cereus*, *Escherichia coli* and *P. aeruginosa*	[133]
Bacillus subtilis	Gold	Antibacterial and antifungal	*C. albicans*, *Shigella sonnie*	[134]
Bacillus thuringiensis	Silver	Antifungal	*A. niger*, *A. terreus*, *A. flavus*, and *A. fumigatus*	[135]
Pseudomonas poae	Silver	Antifungal	*F. graminearum*	[136]
Bacillus sp.	Silver	Antifungal	*F. oxysporum*	[137]
Streptomyces griseus	Copper	Antifungal	*Poria hypolateritia*	[138]
Streptomyces spp.	Copper oxide	Antifungal	*Alternaria alternata*, *Pythium ultimum*, *A. niger* and *F. oxysporum*	[139]
B. thuringensis	Silver	Antiviral agent	*Sun hemp rosette virus*	[89]
B. licheniformis	Silver	Antiviral agent	*Bean yellow mosaic virus*	[94]
Fungi (Mold)				
A. niger	Silver	Antifungal	*Phytophthora infestans*	[83]
A. niger, *A. flavus*, and *P. chrysogenum*	Silver	Antifungal	*A. terreus*, *F. oxysporum*, *P. citrinum*, *Rhizopus stolonifer* and *Mucor mucedo*	[140]
A. terreus	Copper	Antibacterial and antifungal	*B. subtilis*, *S. aureus*, *P. aeruginosa*, *E. coli*, *C. albicans*, *C. glabrata*, *C. tropicalis*, and *C. parapsilosis*	[84]
F. oxysporum	Silver	Antibacterial	*E. coli* and *P. aeruginosa*	[141]
T. viride	Zinc	Antibacterial and antifungal	*S. aureus*, *Bacillus sp.*, *P. aeruginosa*, *Klebsiella sp*, *Acinetobacter baumannii*, *C. albicans*	[142]
A. oryzae and *F. solani*	Silver	Antibacterial	*B. cereus* SBTBC, *Enterococcus faecalis* 8J, *Lesteria monocytogenes* 10403S, *S. aureus*, *E. coli* and *Salmonilla sp*	[143]
P. citrinum	Silver	Antibacterial	*B. subtilis*, *S. aureus*, *E. coli*, and *P. aeruginosa*	[144]
Fungi (yeast)				
Saccharomyces cerevisiae	Silver	Antibacterial	*S. aureus*, *P. aeruginosa*	[145]
S. cerevisiae	Zinc	Antibacterial	*S. aureus* and *E. coli*	[90]
C. glabrata	Silver	Antibacterial and antifungal	*E. coli*, *K. pneomonaie*, *P. aeruginosa*, *S. typhimurium*, *S. flexneri*, *S. aureus*, *Candida sp.*	[146]
Pichia pastoris	Silver	Antibacterial	*S. aureus*, *E. coli*, *Enterococcus faecalis*, and *Klebsiella pneumonia*	[147]
Yarrowia lipolytica	Silver	Antibacterial	*S. aureus*, *E. coli*, *E. faecalis*, *Proteus vulgaris*, *S. pyogenes*, and *P. aeruginosa*	[127]
Algae				
Chlorella vulgaris	Silver and gold	Antibacterial	*S. aureus*, *E. coli*, *Streptococcus sp.*	[148]
Spirulina platensis	Silver, titanium, cobalt	Antifungal	*C. albicans*, *C. glabrata*, and *C. krusei*	[149]
Anabaena spiroides	Gold	Antibacterial	MDR *K. oxytoca* and *S. pyogenes*	[150]
Calothrix membranacea	Silver	Antibacterial	MDR *S. aureus*, *E. coli*	[151]
Lyngbya sp.	Silver	Antibacterial	*S. aureus*, *P. aeruginosa*, *E. coli*	[152]
Tetraselmis indica	Zinc	Antibacterial	*S. aureus*, *E. coli*	[153]

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