



REVIEW ARTICLE

Phage therapy: An eco-friendly technique for managing bacterial diseases in plants

Janakadatta Reddy Kovvuri*, Chanassery Rajendran Rashmi, Ayisha Rehman, Anju Chalbhadhath, Reshmy Vijayaraghavan & Aswini Ajith

Department of Plant Pathology, College of Agriculture, Kerala Agricultural University (KAU), Vellanikkara, Thrissur 680 651, Kerala, India

*Correspondence email - Janakadatta261@gmail.com

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Abstract

Bacterial diseases pose serious threats to crops and conventional chemical treatments not only harm the environment but also contribute to the emergence of antibiotic resistance. Bacteriophage therapy is a targeted and environmentally friendly alternative that specifically eradicates harmful bacteria without affecting beneficial microorganisms. Phages are composed of proteins and nucleic acids, which infect bacteria through either lytic or temperate cycles. While temperate phages are valuable in genetic engineering and diagnostics due to their ability to integrate their genomes, lytic phages, which destroy host cells, are preferred for controlling plant diseases. Environmental factors significantly influence the survival and effectiveness of phages in soil and on plant surfaces. Phage mobility can be restricted by pH, temperature, water content and soil composition. Techniques such as the application of phage-derived proteins (e.g., endolysins), combining phages with antimicrobial agents and the use of phage cocktails have been employed to enhance efficacy. Moreover, phage stability under harsh environmental conditions, particularly UV exposure on leaf surfaces, can be improved through formulations such as encapsulation with protective substances (e.g., corn flour, skim milk). Despite promising results in greenhouse trials, open-field applications remain challenging due to unstable environmental conditions and the rapid decline of phage populations. Since *in vitro* performance often does not correspond with field results, more comprehensive field testing is still required for phage therapy. With continued research and appropriate regulatory support, phages could become effective and sustainable tools for managing plant diseases.

Keywords: disease control; endolysins; holins; lysogenic cycle; lytic cycle; phages

Introduction

Cultivated plants frequently face threats from various pests and diseases. Plant pathogens, such as fungi, bacteria and viruses, can cause serious diseases in crops, resulting in severe economic losses for farmers. It is estimated that plant diseases are responsible for approximately 10–16 % of global crop losses annually, posing a major threat to food security worldwide (1). Of these losses, plant bacterial diseases contribute to approximately 30 % worldwide (2). *Pseudomonas*, *Ralstonia*, *Agrobacterium*, *Xanthomonas*, *Erwinia*, *Xylella*, *Pectobacterium* and *Dickeya* are among the most economically important and destructive bacterial plant pathogens worldwide (3). Several factors make bacterial disease management in crops difficult, including the limited availability and durability of effective bactericides, high pathogen variability, rapid evolution of bacterial populations, frequent genetic exchange and favourable environmental conditions that promote disease development and rapid bacterial multiplication (3). Chemical-based bactericides, particularly copper compounds and antibiotics such as streptomycin and oxytetracycline, have historically been used to manage bacterial diseases in crops (4). Antibiotics have been used in plant disease management since the 1950s, particularly after World War II, but their extensive use has contributed to the emergence of antibiotic-resistant strains in

several plant pathogenic bacteria, raising concerns about long-term efficacy and resistance dissemination (4). Additionally, the widespread use of antibiotics poses risks to human health and the environment (4). Researchers have developed ecological and eco-friendly methods for controlling bacterial plant infections because of these limitations. Numerous alternative disease management tools have been developed for crop protection, including microbial biocontrol agents, plant-derived or microbially derived antimicrobial compounds and plant defence activators that enhance host immunity (5). One promising and re-emerging strategy among these alternative techniques is the utilisation of bacteriophages, viruses that specifically infect and kill bacterial cells, known as phage therapy (3, 6). This review provides an overview of the characteristics of phages, their structure, the early history of phage therapy, methods for phage preparation, application techniques and the potential challenges in using phages to control plant bacterial diseases.

General characteristics of bacteriophages

Bacteriophages (phages) are viruses that infect and replicate host bacteria and archaea (6). Structurally, most phages possess a relatively simple virion organisation consisting of a nucleic acid genome packaged in a protein capsid, often accompanied by a tail and tail fibres that facilitate host recognition and genome delivery

(7) (Fig. 1). Phages are widely dispersed throughout bacterial host-populated environments, such as soil, water, air and the intestines of human and animals (8, 9). Since their discovery more than a century ago, bacteriophages have been thought to be the most diverse and prevalent biological organisms on earth (8). They are crucial for nutrient cycling and bacterial genome evolution (8). Although there are billions of bacteriophages in the environment that infect many kinds of bacteria, the most well-characterised bacteriophages are found in the group *Caudovirales* (6). Phages are classified based on their virion morphology (shape and structural features) and genomic characteristics, including nucleic acid type (DNA or RNA), genome organisation and sequence relatedness (10). Traditionally, tailed phages were grouped into the families *Siphoviridae*, *Podoviridae* and *Myoviridae*, while filamentous phages were classified separately. Phages typically range in size from 20–200 nm, as shown in Fig. 1. Many bacteriophages, particularly tailed phages, possess a head (capsid) containing the genetic material, a tail structure, a base plate and tail fibres that facilitate attachment to the host bacterium (11). Most characterised bacteriophages possess double-stranded DNA (dsDNA) genomes, accounting for approximately 90–95 % of described phages, whereas only a small minority contain single-stranded DNA (ssDNA), single-stranded RNA (ssRNA), or double-stranded RNA (dsRNA) genomes (11).

Life cycles of bacteriophages

Bacteriophages are commonly classified as lytic or temperate based on their replication strategies; lytic phages rapidly replicate and lyse the host cell, whereas temperate phages can establish lysogeny by integrating into or persisting within the bacterial host genome (12). The reproductive cycle of lytic phages (Fig. 2) consists of six stages: attachment, penetration, transcription, biosynthesis, maturation and lysis. This process typically destroys the infected host bacterium (13). Conversely, temperate phages commonly establish lysogeny by integrating their genomes into the host

bacterial chromosome as prophages, which are replicated along with the bacterial genome and transmitted to daughter cells during cell division (12). Environmental stressors such as UV light, high temperatures, ionising radiation, antibiotics or heavy metals may induce temperate phages to enter the lytic cycle and lyse the host bacterium (12). When preparing these phages for downstream therapeutic uses, careful extraction and purification methods must be deployed early on to yield completely endotoxin-free bacteriophage suspensions (14). Once integrated into the host genome, these prophages can significantly influence the evolutionary trajectory and virulence profile of bacterial pathogens, often carrying genes that encode for toxins or fitness factors (15). The bacteriophage infection cycle begins when the phage attaches to specific receptors on the surface of susceptible bacterial cells (16). Following irreversible attachment, the phage transfers its genomic DNA (gDNA) into the host-cell cytoplasm (16) (Fig. 3). This successful delivery of genetic material and subsequent host destruction forms the foundational basis for both historical and modern developments in clinical phage therapy (17). After phage genomic DNA is introduced into the host cell, bacteriophages exploit the host bacterium's transcriptional and translational machinery to synthesise phage proteins during the lytic replication cycle (18). In the later stages of the lytic cycle, bacteriophages produce holins and endolysins, two distinct lysis proteins: holins permeabilise the bacterial inner membrane, allowing endolysins to access and degrade the peptidoglycan layer, thereby lysing the cell and releasing progeny phages (13). During the lysogenic cycle, the bacteriophage genome is maintained either as an episomal element or integrated into the bacterial chromosome as a prophage (18). The prophage is then replicated and transmitted to daughter bacterial cells during cell division (18). Prophages can be induced to enter the lytic cycle in response to environmental stressors, changes in the host's metabolic state, or exposure to certain antibiotics, ultimately resulting in host cell lysis (12).

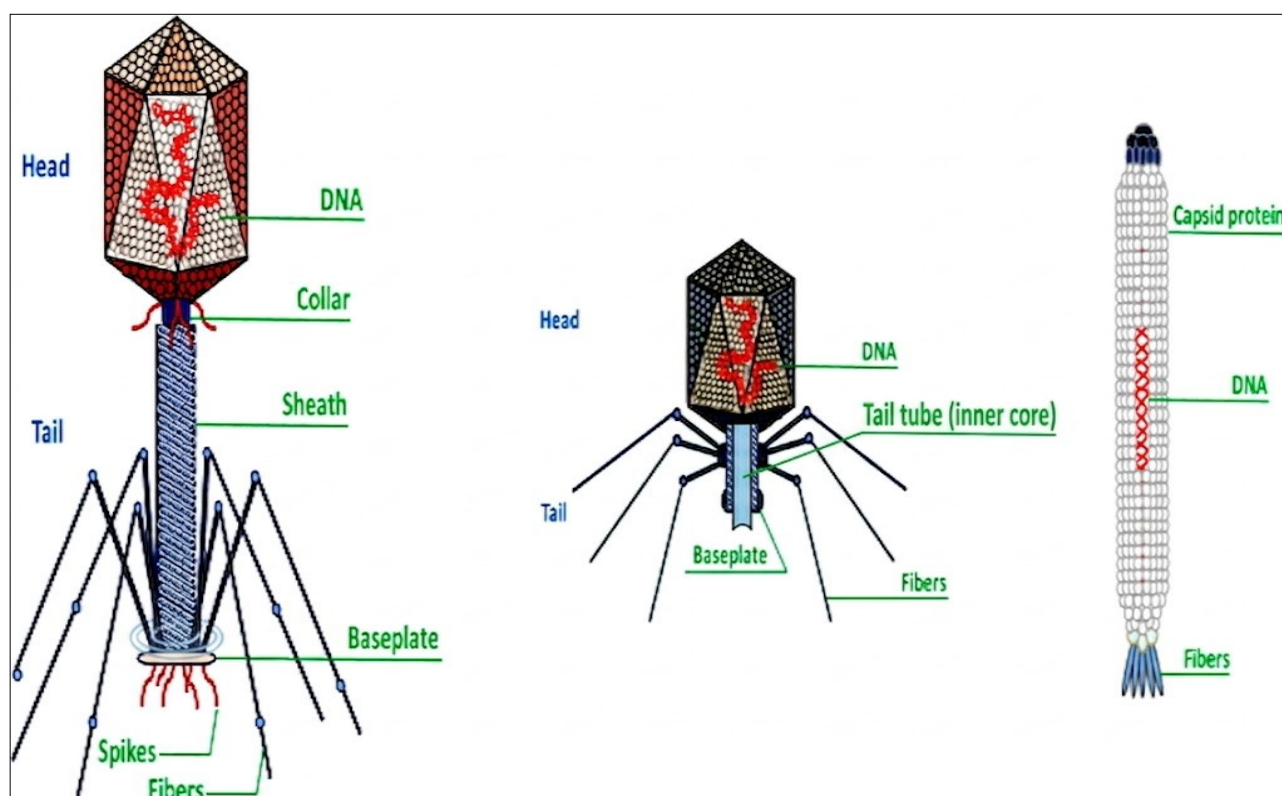


Fig. 1. The structural sketch of bacteriophage (300 dpi resolution). Source: (15).

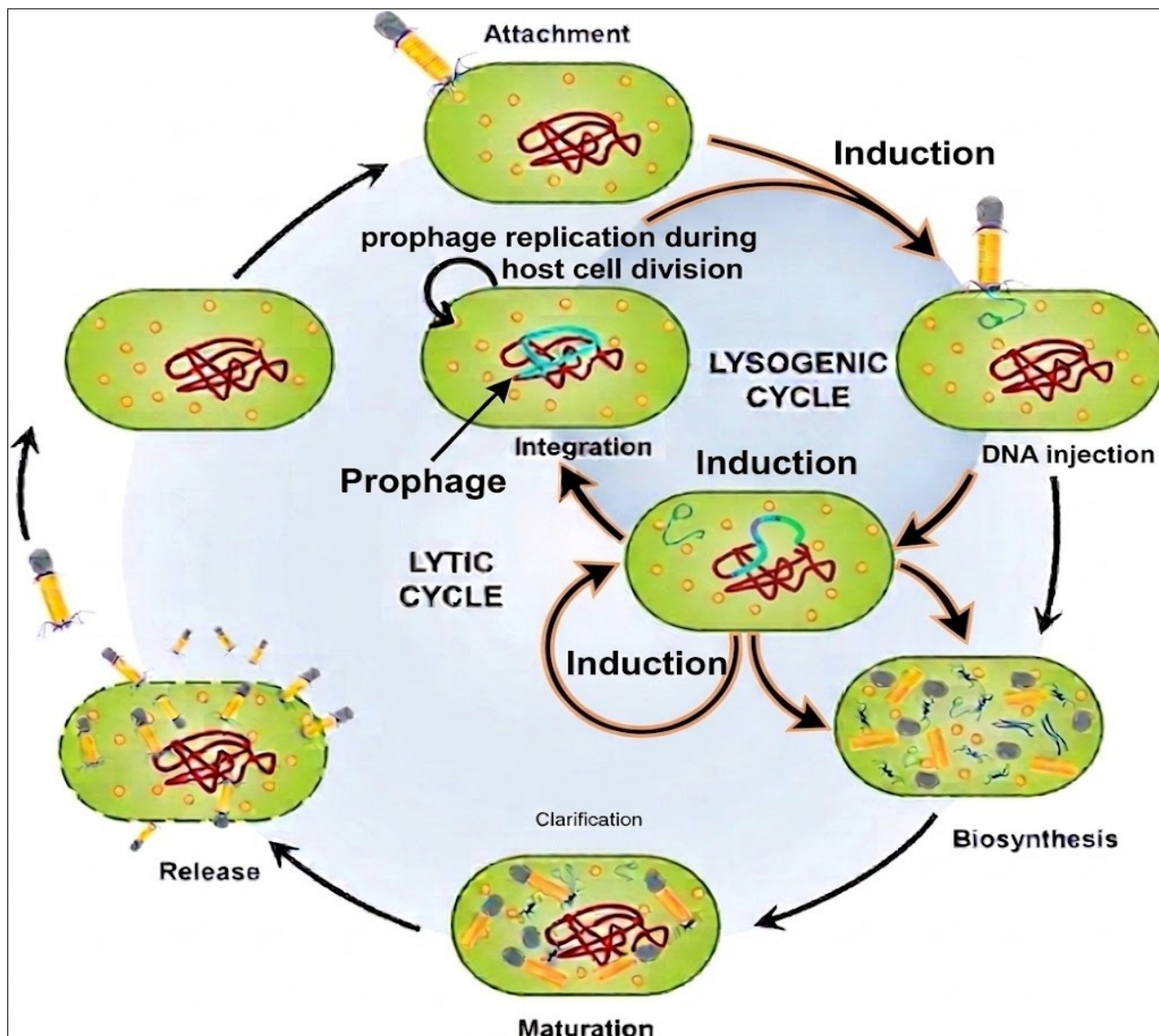


Fig. 2. Lytic and lysogenic cycles of phages (300 dpi resolution). Source: (30).

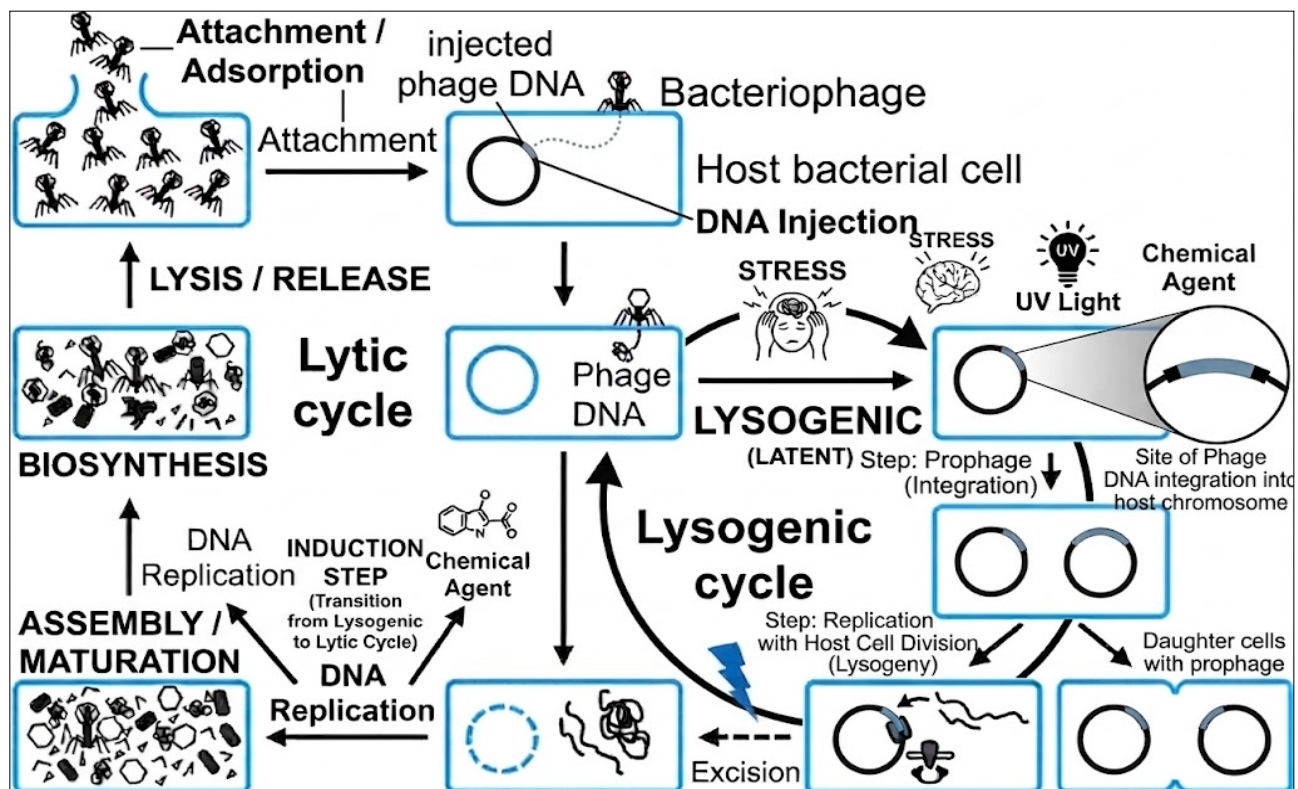


Fig. 3. The general life cycles of bacteriophages (300 dpi resolution). Source: (30).

Phage therapy

Historically, chemical-based bactericides such as copper compounds and antibiotics like oxytetracycline and streptomycin have been used to control bacterial plant infections (4). Antibiotics were initially employed to treat plant diseases after World War II (4). However, numerous plant-pathogenic bacteria have developed resistant strains as a result of the inappropriate use and misuse of these antimicrobial agents, which is highly concerning (2). These limitations have driven the renewed interest in phage therapy as a sustainable and environmentally benign alternative for managing bacterial plant diseases (3). Due to their immediate bactericidal activity and lack of genome integration, lytic phages are preferentially employed for the control of bacterial plant diseases (6). Temperate phages, although generally unsuitable for direct biocontrol because of lysogeny, are more commonly exploited for diagnostic and molecular applications, including bacterial detection (12). Utilising bacteriophages to treat diseases caused by bacteria brought on by pathogens is known as phage treatment (16). It was developed and widely used from the 1920s through the 1940s, before the large-scale production of penicillin began in 1944 (16). Unlike antibiotics, which often target a broad range of bacteria, phage therapy specifically lyses host bacteria, leaving non-host bacterial populations unaffected (17). This precision is a key advantage of phage therapy since it only targets the dangerous bacteria and does not disturb the entire bacterial community. Since bacteriophages depend on susceptible bacterial hosts for replication, phage populations generally decline as host bacterial populations decrease. These phage–host interactions play important roles in regulating microbial population dynamics, community stability and microbial diversity (8). The application of bacteriophages offers two major advantages: they possess a narrow host range, allowing them to specifically target and eliminate only the pathogenic bacteria without affecting beneficial microorganisms (16); and they are self-limiting in the absence of host bacteria, while replicating in their presence. This reduces their impact on the treated environment and soil microbial communities. In recent years, numerous studies have investigated the use of bacteriophages for the biocontrol of important bacterial plant pathogens, with many reporting promising or highly effective disease suppression outcomes (3, 6) (Table 1).

Phage preparation

Bacteriophages are widely distributed in bacteria-rich environments, including hospital wastewater, sewage treatment facilities, rivers and lake waters (18, 19). Once isolated and

enriched, phages can be processed and manufactured. A major challenge in preparing therapeutic bacteriophages is the removal of bacterial contaminants, including exotoxins, nucleic acids, flagella, peptidoglycan fragments, endotoxins and residual culture medium components (20). In Gram-negative bacteria, endotoxins are primarily lipopolysaccharides (LPS), which consist of three major structural components: Lipid A, a core oligosaccharide and the O-specific polysaccharide (O-antigen) (21). The presence of LPS, a major molecule that induces toxicity by triggering a strong innate immune response, including cytokine release, is a primary concern in phages targeting Gram-negative bacteria (21). Therefore, endotoxins must be removed for phage preparations to be safely used in therapy.

Purification, concentration and cultivation of phages

The first step in preparing crude phage lysates involves infecting the target bacterial strain with a specific bacteriophage under suitable growth conditions. Following phage replication and subsequent bacterial cell lysis, a bacterial lysate containing released phage particles, cell debris and bacterial components is obtained (16). After that, the bacteriophage is grown on bacterial cultures in an ideal environment, commonly around 37 °C for several hours to overnight, depending on the phage-host system (16, 22). After infection, the bacteriophage is propagated in actively growing bacterial cultures under appropriate incubation conditions, which commonly include temperatures around 37 °C and incubation periods ranging from several hours to overnight, depending on the host bacterium and phage type (22). Finally, the crude phage lysate is subjected to an appropriate purification procedure to remove bacterial debris, toxins and other contaminants while retaining viable phage particles (20). One purification method involved sequential ultrafiltration of crude bacteriophage suspensions (bacterial lysates) derived from *Pseudomonas aeruginosa* and *Escherichia coli* using a 30 nm polysulfone membrane under elevated pressure (1 bar) (14). The concentrated phage suspension was further purified by chromatography on Sepharose 4B, followed by Matrex Cellulofine Sulphate (14). The concentrated phage suspension was then subjected to gel filtration chromatography on Sepharose 4B, followed by Cellulofine Sulphate affinity chromatography for further purification and endotoxin removal (14). Following partial purification, the phage preparation may be subjected to additional chromatography using Cellulofine sulfate resin to further reduce endotoxins and bacterial contaminants while retaining phage particles (14). The differences in the way the virus interacts with the cellulosic matrix are observable regardless of the virus's size, genetic composition, or presence of a lipid envelope (23).

Table 1. Summary of bacteriophage biocontrol experiments which have been conducted since the year 2000 to the present

Pathogen	Host	Disease	Information
<i>Dickeya solani</i>	Potato	Soft rot	Phage vB_DsoM_LIMEstone1 and vB_DsoM_LIMEstone2 reduced soft rot in inoculated tubers in both bioassays and field trials, resulting in increased crop yield
<i>Ralstonia solanaceum</i>	Tomato	Bacterial wilt	Tomato plants treated with phage 8RSL1 showed no wilt symptoms throughout the experimental period, whereas untreated plants developed symptoms within 18 days post-infection
<i>Xanthomonas campestris</i> pv. <i>vesicatorum</i>	Tomato	Bacterial spot	Field application of phages provided disease control comparable to copper-mancozeb treatment; combined use with acibenzolar-S-methyl (ASM) enhanced disease suppression
<i>Pectobacterium carotovorum</i> ssp. <i>carotovorum</i>	Lettuce	Soft rot	Greenhouse trials demonstrated that phage PP1 significantly reduced disease development in lettuce plants.
<i>Erwinia amylovora</i>	Apple	Fire blight	Phages ΦEa1337-26 and ΦEa2345, when delivered using <i>Pantoea agglomerans</i> as a carrier, reduced infection of detached pear blossoms by 84 % and 96 % respectively. In potted apple tree blossoms, the combination of ΦEa1337-26 and <i>P. agglomerans</i> achieved a 54 % reduction in infection. The level of disease control was comparable to that provided by streptomycin

Endotoxin levels in phage suspensions that ranged from 0.4 to 7 EU/mL were considered acceptable as a result of this purification process (14). Specifically, the purified bacterial lysates had 0.25 EU (endotoxin units) per 10^8 *P. aeruginosa* F8 phage particles and 1.4–2 EU per 10^8 *E. coli* T4 phage particles (14). Achieving these low-endotoxin limits is highly critical when designing therapeutic preparations against Gram-negative targets, particularly because many of these plant pathogens possess an intricate array of intrinsic virulence factors that can exacerbate disease severity if not strictly controlled (24). In this process, crude phage lysates are first filtered through 0.22 μ m membranes to remove bacterial cells and debris, followed by supplementation with $MgCl_2$ and extraction using organic solvents, which results in the formation of a two-phase system for endotoxin reduction (25). The aqueous phase containing the phage particles is subsequently collected and dialysed against 0.15 M NaCl, followed by dialysis against 25 % aqueous ethanol to remove residual organic solvents and other impurities from the phage preparation (25). The organic phase efficiently partitions endotoxins, thereby reducing endotoxin contamination in the phage preparation (24). In the final step, membrane filtration concentrates the phages and removes residual bacterial debris and medium-derived macromolecular contaminants (20).

Analysis of the genome and description of additional phage characteristics

Genome sequencing and bioinformatic analysis are essential steps in the characterisation of therapeutic bacteriophages, enabling the identification of lysogeny-associated genes, toxins, antibiotic resistance determinants and other virulence factors that may compromise safety (22). Sequencing also facilitates rapid differentiation between lytic and temperate phages. Since temperate phages can establish lysogeny within bacterial hosts, they are generally avoided in phage therapy applications (12). Nevertheless, genetic engineering approaches have been explored to remove lysogeny-related functions and improve their therapeutic suitability (26). Bioinformatic analyses additionally permit comparison with previously characterised phages, including those with documented therapeutic outcomes (26). During phage characterisation, parameters such as burst size, latent period,

adsorption rate and thermal or pH stability are also evaluated because these properties influence phage production, storage and therapeutic performance (27). Evaluating these traits is essential because the intrinsic rate of virion decay and the long-term persistence of infectious particles vary greatly depending on how these structural characteristics hold up in the surrounding ecosystem (28). Most bacteriophages remain stable over a moderately broad pH range, although stability varies according to phage type and environmental conditions (27). Morphological characterisation is likewise important for phage classification and detailed study. Transmission electron microscopy (TEM) is commonly used to examine phage morphology and structural characteristics for taxonomic and functional analyses (26) (Table 2).

Factors affecting the effectiveness of phage therapy in soil

Temperature

Temperature is a critical factor that determines the ability of phages to withstand and effectively infect their host (27). For example, daily and seasonal temperature variations affect the *Burkholderia* phages' ability to infect soil environments. Within a temperature range of 30–50 °C, these phages predominantly exhibit lytic cycles, while at cooler temperatures between 15–25 °C, they tend to adopt lysogenic life cycles (27). The isolation of an N4-like phage capable of infecting *Achromobacter* has also been reported previously (29). It was noted that the phage's lytic activity generally decreased between 50 °C and 80 °C. Similarly, phage ϕ OH3, isolated from sediment at Japan's Obama hot spring, infects *Thermus thermophilus* HB8 and demonstrates optimal growth at high temperatures ranging from 70–90 °C (30). These findings collectively highlight the substantial influence of temperature on phage infectivity and activity within soil ecosystems.

pH

Changes in soil pH can influence both bacterial growth and bacteriophage stability, thereby affecting phage persistence and infectivity in soil environments (27). For example, the infectivity of the *Achromobacter xylosoxidans* phage ϕ Axp-3 was reported to be highest near neutral pH and substantially reduced under strongly acidic or alkaline conditions (29). In addition, adsorption

Table 2. General overview of phage discovery and preparation

Basic Steps in Phage Research	Characteristics/Description
Phage isolation	Bacteriophages are isolated from diverse environments, such as aquatic systems (oceans, lakes, rivers), soil, plants, animals, sewage treatment plants and waste originating from human or animal communities, depending on the target bacterial host. Phage collections or banks often document the source of isolation, date and location of collection and are accompanied by scientific publications detailing the isolation procedures and characterisation. The presence of phages is typically indicated by either turbid to clear suspensions in cultures containing specific bacterial hosts or by the appearance of clear or cloudy plaques (phage spots) on agar plates overlaid with host bacterial lawns.
Phage enrichment	Multiple rounds of adsorption-elution-amplification procedures are repeated to enrich and obtain high titres of phages capable of efficiently infecting target bacteria.
Phage purification	Following phage propagation in host bacterial culture, purification is carried out using techniques such as centrifugation, repeated filtration and chromatography methods, including ultrafiltration, dialysis, ion exchange chromatography, affinity chromatography and size exclusion chromatography. The specific purification method depends on the characteristics of the phage being processed. It is essential to avoid contamination with endotoxins and proteases during preparation to ensure the purity and safety of the final phage preparation.
Phage identification and characterisation	Virion Characterisation involves analysis of morphological, physical and chemical properties of bacteriophages. This includes host range, adsorption rate, latent period, burst size and stability under conditions such as temperature, UV exposure, chemical treatments and pH. Structural visualisation techniques include transmission electron microscopy (TEM), scanning electron microscopy (SEM), cryo-electron microscopy (Cryo-EM) and atomic force microscopy (AFM), enabling detailed virion analysis.
Genomic analysis	Genomic analysis of bacteriophages includes gene functional annotation, detection of regulatory elements and host prediction. Functional annotation helps determine the roles of phage genes, including those involved in replication, lysis and host interaction. Prophage analysis reveals integrated phage sequences within bacterial genomes, while regulatory element identification provides insight into gene expression control. Host prediction, based on sequence homology or CRISPR spacer matching, helps determine potential bacterial hosts.

of phages onto soil particles may be influenced by the physicochemical properties of soil colloids, including hydrophobic interactions, which can contribute to phage persistence in the environment (31).

Soil clay

Clay minerals can contribute to bacteriophage preservation by adsorbing phage particles onto mineral surfaces, thereby protecting them from environmental stress and extending their persistence in soils, particularly in the absence of host bacteria (32). Phage adsorption, infectivity and survival are strongly influenced by the physicochemical properties of clay minerals and soil particles (33). Minerals such as kaolinite, montmorillonite and illite can adsorb bacteriophages through electrostatic and cation-bridging interactions, which may alter phage mobility and infectivity (33). Similarly, adsorption of bacteriophage $\phi 6$ onto minerals including goethite, montmorillonite, illite and kaolinite has been reported to reduce infectivity following surface attachment (34). Associations between soil mineral composition and persistence of enteric bacteriophages such as $\Phi X174$ and MS2 have also been documented in environmental matrices (34).

Other elements

Phage infection dynamics in soil bacterial hosts vary according to soil physicochemical properties and nutrient availability (35). In nutrient-limited soils, bacterial populations often exhibit reduced metabolic activity and slower growth rates, which can decrease phage adsorption, replication and overall infection efficiency (35). Soil water content also strongly influences phage persistence, mobility and host-phage interactions within soil environments. Moisture regulates bacterial activity and affects phage diffusion through soil pore networks, thereby altering the frequency of phage-host encounters (36). Consequently, these hydrological conditions dictate the ultimate fate and physical transport of viral particles through porous environmental media, determining whether they remain free to migrate or become trapped within the soil matrix (37).

Techniques for using bacteriophages to control plant diseases

Use of specific bacteriophages

The application of single bacteriophages to plants has been investigated under greenhouse and field conditions using several delivery methods, including soil drenching, foliar spraying, infiltration and seed immersion treatments (Fig. 4) (3). For example, soil drenching with bacteriophages in the rhizosphere significantly reduced bacterial wilt severity in tomato caused by *Ralstonia solanacearum* (38). Similarly, foliar application of bacteriophages effectively reduced disease incidence caused by *Xanthomonas campestris* pv. *campestris* (38). Various methods of bacteriophage application in agriculture are summarised in

Table 3. In addition, filamentous phages have shown promise in disease management. Infection of *R. solanacearum* with the filamentous $\Phi RSM3$ phage reduced bacterial virulence by suppressing the expression of several virulence-associated genes, including *phcA*, *phcB* and *hrpB* (39). Furthermore, tomato plants inoculated with $\Phi RSM3$ -infected bacterial cells exhibited enhanced expression of host pathogenesis-related (PR) genes, including *PR-1a*, *PR-2b* and *PR7*, indicating induction of plant defence responses (39).

Use of bacteriophage cocktails or mixtures

Most bacteriophages infect only specific strains within a bacterial species, although some possess broader host ranges capable of infecting multiple species or genera (40). This specificity is primarily determined by interactions between phage attachment structures and receptors on the bacterial cell surface (41). However, bacteria can rapidly develop resistance to bacteriophage infection through several mechanisms, including modification or loss of phage receptor sites, restriction-modification systems and CRISPR-Cas-mediated degradation of phage nucleic acids (40, 41). For example, phage-resistant mutants of *R. solanacearum* were detected within 30 hr following exposure to lytic phages (41). This rapid adaptation underscores the diverse and sophisticated arsenal of cell-surface and intracellular resistance mechanisms that bacteria deploy to block viral infection (42). To overcome the narrow host range of individual phages and reduce the emergence of phage-resistant bacterial populations, bacteriophage cocktails containing multiple lytic phages have been developed (43). In one study, a cocktail consisting of five host-range mutant bacteriophages lysed all 21 tested strains of *X. campestris* pv. *pelargonii*, including strains resistant to the parent phages, demonstrating the effectiveness of phage mixtures for managing bacterial blight in geranium (43).

Application of bacteriophages with other antimicrobial agents

Numerous studies have explored the synergistic effects of combining bacteriophages with antimicrobial agents such as antibiotics and systemic acquired resistance (SAR) inducers to enhance disease suppression (3). It has been demonstrated that the SAR inducer acibenzolar-S-methyl (ASM), when combined with bacteriophages, provides superior control of bacterial spot on tomato caused by *X. campestris* pv. *vesicatoria* under greenhouse conditions (5). Furthermore, this combination resulted in enhanced disease control efficacy and suppressed the visible hypersensitive response elicited by ASM (44). Similarly, in field studies on bacterial leaf blight of onion caused by *X. axonopodis* pv. *allii*, treatment with a phage mixture and ASM reduced disease severity by 50 %, outperforming a copper hydroxide-mancozeb treatment that achieved a 31 % reduction (45). In greenhouse trials, application of phage K Φ 1 in combination with copper hydroxide significantly reduced lesion

Table 3. Studies employing different methods of phage therapy under greenhouse and field conditions

Pathogen	Host	Disease	Phages	Treatment methods	Test conditions
<i>Dickeya solani</i>	Potato	Soft rot	Monophage VBD1 and 2	Soil drench	Greenhouse
<i>Streptomyces scabies</i>	Potato	Common scab	Monophage AS1	Soil drench	Greenhouse
<i>Ralstonia solanacearum</i>	Tomato	Bacterial wilt	Monophage $\Phi RSL1$	Soil drench	Greenhouse
<i>Pectobacterium carotovorum</i> ssp. <i>carotovorum</i>	Lettuce	Soft rot	Monophage PP1	Spray and soil drench	Greenhouse
<i>X. citri</i> ssp. <i>citri</i>	Citrus	Canker	Cocktail (NJ-P3)	Spray and soil drench	Field
<i>R. solanacearum</i>	Tomato	Wilt	Cocktail(P23M1)	Spray	Field

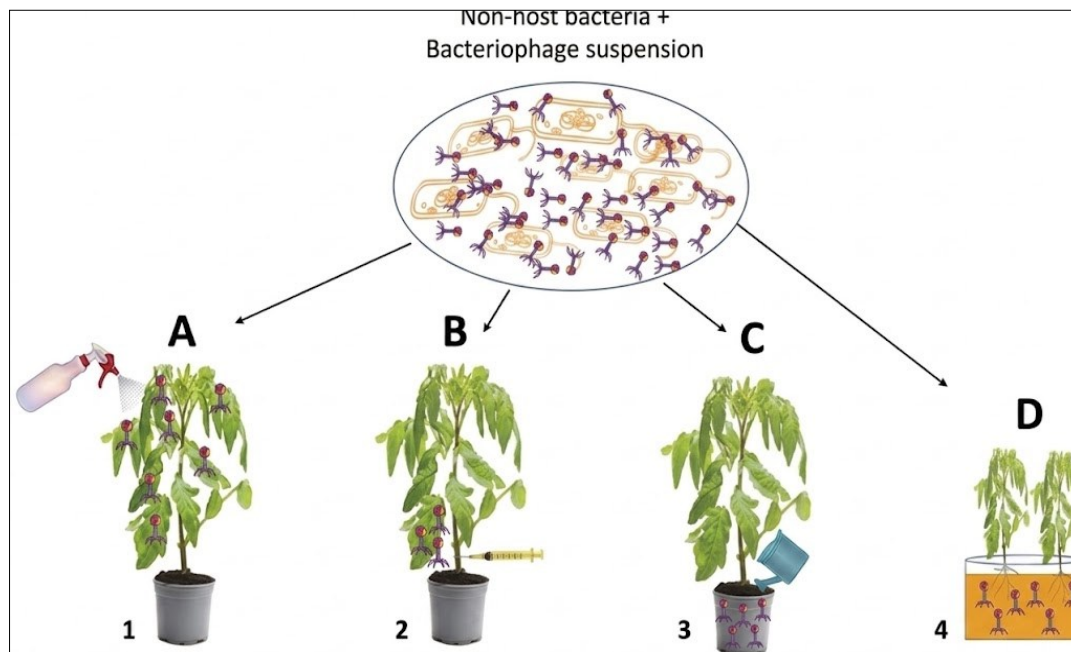


Fig. 4. Techniques for bacteriophage treatment in a field or greenhouse. (A) Foliar spray: phage solution was directly added into the base of the plant; (B) direct infiltration into plant tissues; (C) Soil mixture drenching; (D) immersion of seedlings or seeds: the seedlings or seeds can be immersed in phage solution before planting. Source: (38).

numbers of *X. euvesicatoria* on pepper leaves, with reductions ranging from approximately 81 % to 90 % across multiple experiments (46).

Use of endolysins, which are proteins derived from bacteriophages, as antimicrobial agents

Bacteriophages are widely distributed in bacteria-rich environments, including hospital wastewater, sewage treatment facilities, rivers and lake waters (18, 19). Once isolated and enriched, phages can be processed and manufactured. A major challenge in preparing therapeutic bacteriophages is the removal

of bacterial contaminants, including exotoxins, nucleic acids, flagella, peptidoglycan fragments, endotoxins and residual culture medium components (20). Since traditional co-precipitation can fail to separate these impurities without compromising viral structural integrity, modern workflows rely on a comparative selection of specialised, multi-step extraction strategies tailored to the target phage type (47). Standardising these complex purification steps remains a critical step for scaling up both personalised therapies and agricultural biocontrol products (48, 49) (Fig. 5). Ultimately, establishing robust, high-yield

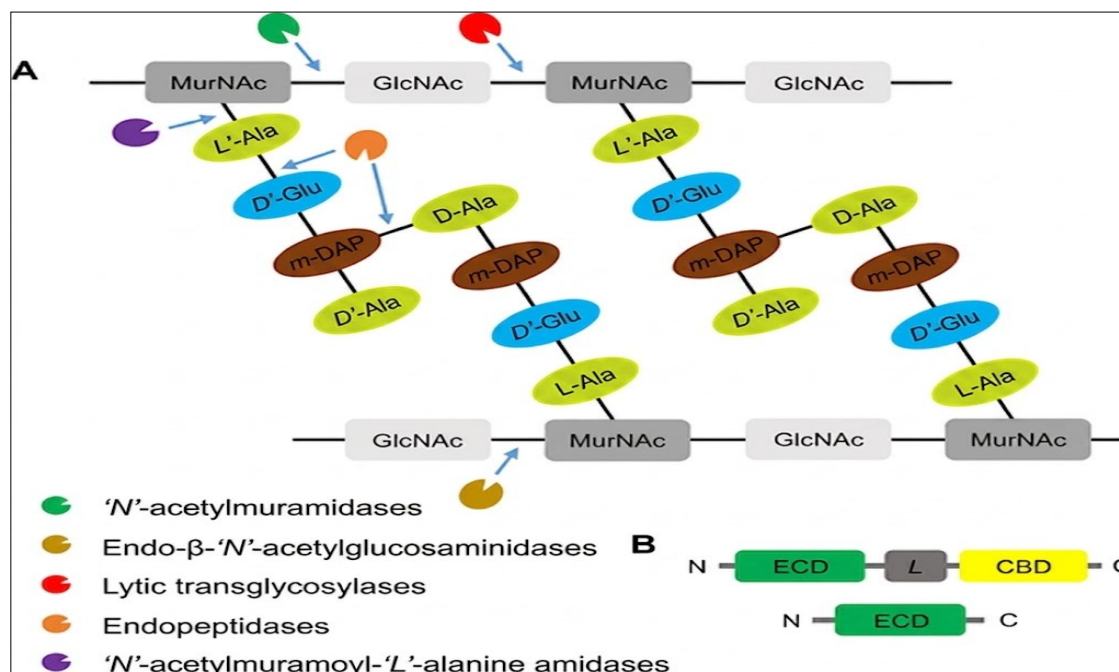


Fig. 5. Endolysin mechanisms and architectures. (A) Cleavage sites of five endolysin classes on the peptidoglycan framework. Blue arrows indicate specific bonds targeted by glycosidases (N -acetylmuramidases, endo- β - N -acetylglucosaminidases and lytic transglycosylases), N -acetylmuramoyl- L -alanine amidases and endopeptidases within the glycan backbone and peptide side chains (L -Ala, D -Glu, m -DAP, D -Ala). (B) Architectural variety of endolysins. The top structure illustrates the modular configuration typical of Gram-positive phages, featuring an enzymatic catalytic domain (ECD) connected by a flexible linker (L) to a cell-wall-binding domain (CBD). The bottom structure illustrates the globular, single-ECD architecture characteristic of most Gram-negative phage endolysins, provided here for structural comparison. (300 dpi resolution). Glu, glutamic acid; Ala, alanine; DAP, diaminopimelic acid. Source: (48).

purification protocols is paramount to overcoming clinical development hurdles and ensuring that the final phage suspensions are safe, stable and highly regulatory-compliant for open field or therapeutic applications (46, 50).

Current targets and management strategies for phage-based phytopathogen control

Ralstonia solanacearum

Ralstonia solanacearum is a destructive soil-borne Gram-negative bacterium capable of infecting more than 200 plant species belonging to over 50 botanical families (51, 52). Historically, strains of *R. solanacearum* were classified into races according to host range and biovars based on carbohydrate utilisation patterns. However, this phenotypic classification system has largely been replaced by the modern *R. solanacearum* species complex (RSSC) framework, which classifies strains into phylogenetically informative groups including phylotypes, sequevars and species-level lineages (53). The pathogen causes economically important diseases such as bacterial wilt and potato brown rot in crops including tomato, tobacco, banana and potato (54). Infection generally begins through the invasion of plant roots, followed by colonisation of xylem vessels. Common symptoms include wilting, chlorosis, stunted growth, vascular discolouration and eventual plant death, although latent or asymptomatic infections may also occur (54). Current management practices include crop rotation, use of pathogen-free planting material, resistant cultivars, sanitation measures and adjustment of planting schedules (35).

***Xanthomonas* species**

The genus *Xanthomonas* belongs to the class Gammaproteobacteria and includes numerous phytopathogenic species and pathovars differentiated primarily by host specificity and pathogenic characteristics (55, 56). Members of this genus infect a wide range of economically important crops, including rice, citrus, banana, tomato and pepper (57, 58). *Xanthomonas* species typically colonise either vascular tissues such as the xylem or non-vascular intercellular spaces within mesophyll tissues, exhibiting considerable tissue and host specificity (58). Bacterial spot disease of tomato and pepper, caused by *X. campestris* pv. *vesicatoria* and related *Xanthomonas* species, has been reported worldwide and can result in substantial yield and quality losses, especially under warm and humid conditions (59). The pathogen enters plants through stomata or wounds and subsequently colonises intercellular spaces, producing water-soaked lesions that later become necrotic and may lead to defoliation and heavily spotted fruits (60). Management strategies include the use of pathogen-free seeds and transplants, sanitation practices, avoidance of mechanical injury, copper-based bactericides, antibiotics such as streptomycin and resistant cultivars (59). However, resistance to copper compounds and antibiotics has been widely reported among *Xanthomonas* populations and resistant cultivars often provide inconsistent protection under field conditions (60).

Erwinia amylovora

Fire blight is a destructive disease affecting members of the Rosaceae family and is caused by *Erwinia amylovora*, a Gram-negative bacterium belonging to the family Enterobacteriaceae (24). During infection, the pathogen commonly enters susceptible plants through floral nectaries, although wounds and natural openings can also serve as entry

sites (61). Following entry, the bacterium colonises intercellular spaces and vascular tissues, eventually spreading systemically through the plant (24). Under favourable environmental conditions, fire blight symptoms include blossom blight, shoot dieback, tissue necrosis, wilting and canker formation (62). Unlike many phytopathogenic bacteria, *E. amylovora* relies less on extensive cell wall-degrading enzymes and instead depends heavily on production of the exopolysaccharide amylovoran, biofilm formation, motility, quorum sensing and a type III secretion system for virulence and host colonisation (24, 63). Management strategies traditionally include pruning and destruction of infected tissues, sanitation practices and preventive applications of copper compounds or antibiotics such as streptomycin and oxytetracycline (24, 59).

Possible challenges in employing bacteriophages to manage bacterial infections in plants

Although laboratory studies have demonstrated the promise of bacteriophages as biological control agents, successful field application remains challenging because of environmental and ecological constraints (64, 65). Phages are commonly applied either by soil drenching to target the rhizosphere or by spraying onto aerial plant surfaces (the phyllosphere). In soil environments, water availability strongly influences phage dispersion, whereas adsorption to soil particles or entrapment within biofilms can limit phage mobility and persistence (66). Conditions in the phyllosphere further reduce phage survival because exposure to desiccation, temperature fluctuations and solar radiation can rapidly inactivate virions (67).

Numerous laboratory and field studies have shown that high temperatures, extreme pH conditions and sunlight exposure, particularly UV-A and UV-B irradiation, significantly reduce bacteriophage viability (68, 69). Under open-field conditions, phage populations often decline rapidly and may become nearly undetectable within 36–48 hr after application (70). To improve phage stability and efficacy, several formulation and encapsulation strategies have been investigated using materials such as skim milk, casein, corn flour and lignin-based carriers (71, 72). In addition, factors including indigenous microbial communities, phage concentration, virion decay rates, timing of application and environmental conditions can strongly influence the success of phage-based disease management (73). For example, bacteriophages active against *Pseudomonas syringae* pv. *porri* reduced symptom severity under controlled laboratory conditions but failed to provide significant disease suppression in field trials (74). In contrast, the jumbo phage ΦRSL1 effectively suppressed *R. solanacearum* populations and restricted bacterial movement within tomato roots despite exhibiting slower *in vitro* lytic activity than other isolated phages (73). ΦRSL1 also provided prolonged disease protection for up to four months, unlike more rapidly lytic phages (73). Similarly, the filamentous phage XacF1 reduced the virulence of *X. axonopodis* pv. *citri* by decreasing extracellular polysaccharide production and bacterial motility; infection with XacF1 was also associated with the formation of smaller and more turbid plaques during plaque assays (39).

Future perspectives of bacterial virus usage in plants

Numerous studies have demonstrated that bacteriophages can effectively control bacterial infections in plants, with particularly promising outcomes under controlled conditions such as greenhouses (70, 71). However, translating these results to

Table 4. Commercial formulations of bacteriophages

Company	Trade name	Bacteria	Disease management
Omnilytics	Agriphage (Tomato)	<i>Xanthomonas campestris</i> pv. <i>vesicatoria</i> ; <i>Pseudomonas syringae</i> pv. <i>tomato</i>	Bacterial spot and bacterial speck on tomato
Environvest (Hungary)	Erwiphage	<i>Erwinia amylovora</i>	Fire blight of apple
APS Biocontrol Ltd. (Scotland)	Biolyse	<i>Pectobacterium carotovorum</i> subsp. <i>carotovorum</i>	Soft rot of potato

open-field agriculture remains challenging (65, 67). Unlike controlled environments, field conditions are highly variable and influenced by temperature fluctuations, ultraviolet radiation, rainfall, soil composition and microbial competition (65, 67). Despite encouraging research over recent decades, commercially available bacteriophage products for plant disease management remain limited (70) (Table 4). Although these products demonstrate the feasibility of phage-based crop protection, their market penetration is still modest (69). This limitation reflects not only technical challenges, such as formulation stability, delivery optimisation and host range specificity, but also broader structural barriers (74, 77). Environmental variability remains one of the most critical determinants of bacteriophage performance (67). Phage sensitivity to UV radiation, desiccation and temperature extremes necessitates the development of improved formulations, such as encapsulation systems, UV protectants and carrier-based delivery strategies (71, 72). Currently, only strictly lytic bacteriophages are recommended for plant disease management due to safety concerns associated with temperate phages and their lysogenic cycles (17). However, this restriction may overlook potential innovative applications. Temperate phages, although generally unsuitable as biocontrol agents in their native form, have been explored experimentally as engineered virulent derivatives or as delivery vectors for genetic cargo that attenuates bacterial virulence or restores antibiotic susceptibility (75, 76). Non-technical challenges may ultimately determine the trajectory of phage-based plant protection. Regulatory frameworks for bacteriophages vary significantly across countries and are often designed for conventional chemical pesticides rather than biological agents (77). The absence of harmonised global guidelines can slow product approval, increase development costs and discourage investment (77). Furthermore, regulatory uncertainty regarding genetically engineered phages adds another layer of complexity, particularly in regions with strict biotechnology policies (75). Public perception and acceptance also represent critical factors. In parallel, economic considerations, such as production scalability, formulation shelf life, intellectual property protection and cost competitiveness compared to conventional bactericides, must be addressed to ensure commercial viability (75, 78).

Conclusion

Viruses known as bacteriophages are abundant, diverse and specifically infect bacteria. They play important roles in bacterial evolution, ecology and population control. Bacteriophages exhibit either lytic or temperate life cycles; lytic phages kill their bacterial hosts, whereas temperate phages integrate into host genomes. They are promising biocontrol agents in agriculture due to their specificity. Strategies such as phage encapsulation and the use of phage combinations (cocktails) are being explored to extend their antibacterial spectrum while increasing persistence. Furthermore, the potential applicability of temperate phages in diagnostic and therapeutic settings may be enhanced by genetic engineering.

Phage-derived enzymes, such as endolysins, offer innovative alternatives to traditional control methods. Standardised selection criteria, comprehensive purification and stringent field testing are necessary for the effective application of phage therapy. With further advancements alongside appropriate regulatory frameworks, bacteriophage-based solutions have the potential to become effective, sustainable tools for managing plant diseases.

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Authors' contributions

JRK drafted the manuscript. CRR and AR reviewed and revised the manuscript. AC, RV and AA supervised the study. All authors have read and approved the final manuscript.

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