



Review

# Microbial and Plant-Based Compounds as Alternatives for the Control of Phytopathogenic Bacteria

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**Abstract:** Plant pathogens pose a significant threat to agricultural productivity and food security worldwide. The use of traditional chemical pesticides for plant disease management raises concerns due to the emergence of pesticide resistance and their potential adverse effects on human health and the environment. As a result, there is a growing interest in exploring alternative approaches for plant disease control. This review provides an overview of the antimicrobial potential of some plant-derived compounds, including essential oils, plant extracts, wastes and their major constituents, against plant pathogenic bacteria. The antimicrobial activity is attributed to the diverse chemical composition of these plant-derived compounds and their ability to target multiple cellular processes in pathogens' cells. Furthermore, the review explores the use of some antagonistic bacteria and fungi as control tools. These beneficial microorganisms have shown promising results in suppressing the growth of plant pathogens through various mechanisms such as competition, antibiosis and induced systemic resistance. This review discusses the advantages and limitations of using plant-derived compounds and antagonistic microorganisms for plant disease management. Moreover, it highlights the need for further research to optimize their efficacy, develop sustainable formulations and evaluate their performance under field conditions.

**Keywords:** agricultural wastes; antagonistic microorganisms; antimicrobials; essential oils; plant disease control; plant pathogens



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## 1. Introduction

In the vast realm of bacterial species, more than a hundred have been identified as plant pathogens, accounting for a fraction of the tens of thousands to billions of bacterial species known [1,2]. Among them, the most troublesome and widely distributed plant pathogenic bacteria primarily belong to the Gram-negative taxa *Xanthomonas*, *Agrobacterium*, *Pseudomonas*, *Xylella* and *Erwinia*. Gram-positive phytopathogenic bacteria are represented by genera such as *Arthrobacter*, *Clavibacter*, *Curtobacterium* and *Rhodococcus*. These bacteria exhibit a broad host range, infecting a variety of economically important herbaceous and woody plant species [2], resulting in reduced crop yields and diminished product quality. Although quantifying the exact magnitude of yield losses caused by bacterial infections is challenging, it is estimated that plant diseases account for 10–16% of total global plant production losses [2,3] and economical losses of over one billion dollars annually [4]. Notably, the genus *Xanthomonas* alone has been implicated in approximately 350 diseases affecting around 400 different plant species [5–7]. The relative importance of numerous phytopathogenic bacterial species with descriptions of specific hosts and diseases

is discussed by Mansfield et al. [8]. Specifically, the most significant harmful bacteria from both economic and scientific perspectives are those belonging to the *Pseudomonas syringae* complex, *Ralstonia solanacearum*, *Rhizobium radiobacter*, different strains of *Xanthomonas* bacteria and *Clavibacter michiganensis* subsp. *michiganensis*.

The extent of damage that these bacterial species can inflict on agriculture largely depends on their epidemiology and the biological factors that determine their virulence. Bacteria can reside as epiphytes or endophytes in plants, leading to infections and manifesting in symptoms such as chlorosis, necrosis, knots, lesions and overall decline in plant health. These infections can sometimes remain latent or asymptomatic [9–12]. Predominantly Gram-negative plant pathogenic bacteria possess specific virulence factors that enable them to overcome plant defense mechanisms. These factors include toxin production, quorum sensing, two-component signal transduction (TCST) systems and other biological mechanisms [13–16]. To ensure their survival and successful infection, pathogenic bacteria have evolved strategies to manipulate the host defense responses by interfering with hormone signalling pathways. For instance, bacteria such as *R. radiobacter* and *Pseudomonas savastanoi* pv. *savastanoi* synthesize cytokinins and auxins, which serve as carbon and nitrogen sources, while also inducing infection symptoms. These hormones can disrupt normal plant growth and development [13]. Another example is *P. syringae*, which produces a phytotoxin called coronatine. Coronatine enhances bacterial growth and facilitates systemic spread within the host by mimicking the plant hormone jasmonic acid (JA). Interestingly, JA typically functions in plant defense responses against herbivores and necrotrophic pathogens. However, by producing coronatine, bacteria suppress the synthesis of salicylic acid (SA), a plant hormone that is effective against biotrophic and hemibiotrophic pathogens such as bacteria [17,18]. Plant pathogenic bacteria are predominantly classified as hemibiotrophic, displaying a lifestyle in which they initially infect and colonize living host tissue and subsequently transition to surviving in dead plant tissue. However, exceptions to this pattern exist, such as the tumor-inducing bacterium of the genus *Agrobacterium/Rhizobium*, which exclusively thrives in living plant tissue [14]. From an epidemiological perspective, successful plant pathogenic bacteria possess a range of essential traits for their survival and establishment within their hosts. These traits also include motility, signalling mechanisms, adhesion capabilities and the ability to degrade plant-derived compounds.

Phytopathogenic bacteria coexist with beneficial bacterial communities within and on plant hosts that could interfere with the virulence level of pathogenic bacterial species and the severity of diseases. The interaction between pathogenic and beneficial bacteria has been suggested to influence the overall condition and health of plants. However, the precise association and interaction between the plant microbiota and plant health are still not fully understood [19,20]. The emerging field of socio-microbiology has been developed to study these interactions and associations among microorganisms, recognizing their importance as a valuable tool in biodiversity preservation [21]. Considering the coexistence of diverse microbial populations, the application of environmentally friendly preparations for plant protection has become a necessity. By exploring and understanding these complex microbial interactions, eco-friendly approaches can be developed to mitigate the impact of pathogenic agents on plants.

Bacterial disease management is faced with many limitations, one being the lack of effective registered bactericide preparations. Copper-based products can be used to control bacteria that are not resistant to copper, but they can have negative effects on beneficial bacteria and plants [22]. The major concern with the use of antibiotics in plant protection is the occurrence of multidrug resistance of bacteria through horizontal gene transfer or mutations, which have been reported in the literature [23]. To address these challenges, the cultivation of genetically modified plants is regarded as a potential strategy for disease control. Nevertheless, plant modifications, including genetic modifications, are subject to rigorous public scrutiny because of concerns about their perceived unnaturalness and possible hazards, analogous to the employment of synthetic pesticides in agriculture [3]. In

response to the stringent modern demands and the environmental consequences associated with the use of synthetic pesticides and excessive nutrients, the development of alternative and environmentally friendly preparations is essential for sustainable agricultural production, one of the most important sectors of the Sustainable Development Goals [24]. Green preparations, which are environmentally and economically advantageous, offer a solution for agriculture and the control of plant diseases [25]. These preparations aim to provide effective disease control while minimizing environmental impact and promoting sustainable farming practices. Biopesticides are natural products that are categorized as microbial and biochemical biopesticides used to control pests and diseases. These preparations occupy a total of 5% of the global pesticide market with environmentally favourable properties such as biodegradation and selective action against targeted organisms. The largest share among biopesticides is those based on microorganisms, with approximately 90% of available preparations based on entomopathogenic bacterial species and few preparations against fungal and bacterial pathogens of vegetables, fruits and ornamental plants, e.g., *Botrytis*, *Sclerotinia*, *Fusarium*, *Alternaria*, *Xanthomonas*, etc. [26]. However, biochemical biopesticides may eventually prevail in the market, owing to their wider spectrum and stability of preparations in contrast to living microorganisms, which often encounter problems in practice because of their limited availability, slow action and high cost. Biochemical biopesticides could be formulated using essential oils (EOs), plant secondary metabolites, polyphenols, etc. [24]. Although plants employ diverse defense mechanisms to combat pathogens, polyphenols play a crucial role as constituents of the plant cell wall structure and act as barriers in the plant defense system [15,27]. Specifically, polyphenols exhibit toxicity towards bacteria and can inflict damage to microbial cell membranes [28], and thus are promising as active molecules for the development of biochemical biopesticidal products. Consequently, numerous studies highlight the potential application of EOs and plant extracts in plant disease control. According to a review by Wińska et al. [29], EOs have well-established antibacterial activity. Other studies demonstrate the antibacterial potential of plant waste products that are produced in large quantities in agricultural and food production industries, due to the high content of phenolic compounds with antimicrobial properties. Some of these are olive and grape wastes, and fruit and vegetable peels [30]. This review examines the antimicrobial potential of plant-derived compounds, such as EOs, plant extracts and their main constituents, against bacterial plant pathogens. It evaluates their effectiveness, explores their mechanisms of action, and assesses their suitability as eco-friendly alternatives for plant disease management. It also investigates the use of some antagonistic bacteria and fungi as control measures. The review aims to summarize the current knowledge, identify the most promising compounds and microorganisms and their sources, discuss their mode of action, address any limitations or challenges, and suggest future research directions in this field.

## 2. Antagonistic Microorganisms and Microbial Biopesticides

### 2.1. Potential of Some Antagonistic Fungal Strains against Phytopathogenic Bacteria

In recent studies, several filamentous fungi have been investigated as potential biological control agents against pathogenic microorganisms. These studies, comprehensively discussed by Poveda and Baptista [31], have highlighted the antibacterial effects of tested fungi. From the perspective of socio-microbiology, it has been observed that fungi compete with economically important bacteria such as *Xanthomonas*, *Pseudomonas*, *Xylella fastidiosa* and *Rhizobium radiobacter* through various mechanisms including parasitism, antibiosis and competition for space and nutrients. The presence of certain fungal species, mainly belonging to the genera *Trichoderma*, *Epiccocum*, *Drechslera* and *Alternaria*, has been found to positively impact the plant's defense as they establish beneficial interactions with the plant. These fungi have the potential for the biological control of certain bacterial pathogens. In one study, the fungal strain of *Fusarium tricinctum* and its metabolites demonstrated antibacterial potential against *P. syringae* pv. *actinidiae* (bacterial canker in kiwifruit). The fungus alone suppressed bacterial growth by 59.5% in vitro, while its metabolites (imidazole al-

kaloids and enniatins) were active at MIC range from 25 to 50 µg/mL [32]. This finding highlights the potential of fungal-derived compounds as effective agents against bacterial pathogens. Another study [33] investigated the antibacterial activity of 17 morphotypes of orange endophytic fungi, where several strains belonging to the genera *Fusarium*, *Diaporthe*, *Colletotrichum*, *Geotrichum*, *Penicillium* and *Polyporus* exhibited significant antibacterial activity against *X. citri* subsp. *citri*, the causative agent of citrus canker. Notably, *Geotrichum* sp. (gc-1-127-30) and *Diaporthe biconispora* (gc-1-128-79) strains showed the strongest efficacy for inhibiting bacterial growth with MIC of 62.5 and 31.3 µg/mL. Interestingly, individual compounds of *D. biconispora* extracts were significantly variable as antimicrobials, showing a MIC range from 12.5–>1000 µg/mL. The lowest MIC was determined for an unidentified compound (compound 2), suggesting the need for its further identification and evaluation as a control agent of pathogenic bacteria. *Trichoderma* is one of the most commonly encountered genera of biocontrol fungi on the market.

While it exhibits some level of antibacterial activity in vitro, *T. longibrachiatum* is effective against various foodborne bacteria. However, it also suppresses the growth of beneficial bacteria such as *P. fluorescens* and *Bacillus subtilis*, which benefit the host by inducing stress resistance, antibiosis and metabolite synthesis [34]. Moreover, the use of trichokonins derived from *T. koningii* SMF2 has been reported to inhibit the growth of the Gram-positive bacterium *C. michiganensis* subsp. *michiganensis*, the causal agent of bacterial wilt in tomato. However, its efficacy has been limited against Gram-negative plant pathogens such as *Ralstonia solanacearum* and *Erwinia carotovora* [35]. These studies demonstrate the diverse antimicrobial potential of various fungal species and their metabolites against bacterial pathogens. Notably, some fungal strains showed a selective action against targeted bacterial strains, and thus could be implemented as control agents without interfering with natural populations of beneficial microorganisms. Further research is needed to explore and evaluate their efficacy in controlling bacterial diseases in agricultural and horticultural settings.

## 2.2. Potential of Some Antagonistic Bacterial Strains and Bacteriophages against Phytopathogenic Bacteria

Plant growth-promoting bacteria (PGPB), such as certain strains of *Streptomyces*, *Bacillus* and *Pseudomonas*, have been extensively studied for their ability to promote plant growth and act as biocontrol agents against plant pathogens. Among the antagonistic bacteria studied for their suppressive effects on phytopathogenic organisms, the genera *Pseudomonas*, *Bacillus*, *Azospirillum* and *Streptomyces* have received significant attention. *P. fluorescens* and *Streptomyces* spp. are among the most extensively studied biopesticide bacteria. Some *Streptomyces* strains produce antibiotics that can suppress the growth of plant pathogens, while *Bacillus* and *Pseudomonas* strains produce other secondary metabolites such as phytoalexins to inhibit the growth of microorganisms [36]. These bacteria have been found to also stimulate the natural resistance of host plants while exerting antibiosis and competing for nutrients and space with pathogens [37–45]. Soil-dwelling bacteria of *Streptomyces* spp. are known for their production of diverse antibiotics, including streptomycin. Streptomycin has been widely used to control bacterial diseases, particularly for managing the fire blight of apples and pears in antibiotic-approved agricultural regions [46]. The bacterium *P. fluorescens* produces metabolites and enzymes that reduce the growth of pathogenic bacteria and fungi in the soil and on the surface of plant organs, which is a characteristic trait of fluorescing *Pseudomonas* species. In a recent study [47], the researchers investigated the antagonistic properties of bacterial isolates obtained from healthy olive leaves against a *Pseudomonas savastanoi* pv. *savastanoi*. Out of the 46 isolates tested, five exhibited antagonistic activity in vitro. Notably, *Bacillus* sp. Og2 and *P. fluorescens* Oq5 showed the highest inhibition of *P. savastanoi* growth. Furthermore, the secondary metabolites of these isolates demonstrated inhibitory effects after approximately 6 days of incubation. These findings align with numerous studies on the antagonistic activity of bacteria against various plant pathogenic bacterial species, including *R. solanacearum*,

*X. axonopodis* pv. *malvacearum*, *E. amylovora*, *R. radiobacter*, *P. syringae*, *X. arboricola*, *Pectobacterium carotovorum* and *Clavibacter michiganensis*, on different plant hosts, e.g., apple, pear, cotton and apricot [48–51]. Previous studies have suggested that the antagonistic activity of *P. fluorescens* may be attributed to the secretion of minor phenolic compounds [49].

In recent discussions, the effective use of antagonistic bacteria, such as *B. subtilis* 2515-1 against *P. savastanoi* pv. *savastanoi*, the causal agent of olive knot disease, has gained attention [52]. These antagonistic bacteria have been found to produce various enzymes and secondary metabolites, resulting in a greater reduction in knot weight compared with standard copper-based preparations. Specifically, *B. subtilis* 2515-1 reduced the knot weight by 50%, whilst a reduction of 37% was achieved using 0.5% copper sulphate preparation. Notably, the antagonistic bacterial strain *B. subtilis* F1 has shown relative heat resistance, which is advantageous in regions with high temperatures (up to 40 °C) during the vegetation period [53], suggesting the further examination of promising *Bacillus* species to be implemented as control agents in arid regions. Additionally, other antagonistic strains, including *B. megaterium*, *P. koreensis* and *B. pumilus*, have been examined recently for their inhibitory effects on the causal agent of olive knot disease, with inhibition of knot formation ranging up to 65% [54]. However, the efficacy of bacterial inhibition is strongly dependent on the specific bacterial strain tested in vitro, in planta and in vivo [20,52]. In a study by Mina et al. [20], *B. amyloliquefaciens* exhibited the highest antagonistic potential among 27 bacterial strains, inhibiting the growth of *P. savastanoi* pv. *savastanoi* by 26.8% and reducing overall disease severity by 43.7% in in planta experiments. Furthermore, *B. amyloliquefaciens* demonstrated beneficial effects on the host, promoting dry shoot weight (+55%) and root water content (+39.6%). Thus, *B. amyloliquefaciens* shows promise as an efficient ecological solution for the management of olive knot disease, which is prevalent in olive-growing arid regions worldwide. Moreover, in a recent study by Broniarek-Niemiec et al. [55], the application of commercial preparations containing bacterial strains, specifically *B. amyloliquefaciens*, demonstrated inhibitory effects on the incidence of bacterial canker caused by *P. syringae* in cherry orchards in Poland over two growing seasons. Although the efficacy of tested microbial-based preparations was lower than conventional copper and aluminium-fosetyl-based treatments, their effectiveness was still observed.

Bacteriophages, also known as phages, are viruses that specifically target and infect bacteria. They can be employed as a biocontrol agent to selectively eliminate pathogenic bacteria while preserving beneficial microbial communities. The use of bacteriophages shows promise in the field of bacterial disease management due to their high specificity and ability to evolve alongside bacterial populations. Phage-based preparations are used in some agricultural regions against *X. campestris* pv. *vesicatoria* and *P. syringae* pv. *tomato*, *C. michiganensis* subsp. *michiganensis*, *E. amylovora* and *X. citri* subsp. *citri*, as well as soft-root bacteria [56]. According to the review by Buttmer et al. [57], experiments conducted using bacteriophages are focused on various phytopathogenic bacterial species listed among the top 10 pathogenic bacteria in molecular plant pathology [8], such as *Pseudomonas syringae* pv. *porri* causing bacterial blight of leek, resulting in a reduction of disease severity in field trials. Moreover, phages were studied against *Xanthomonas* species, which are infectious to tomatoes, onions, grapefruit and oranges. Most of these studies were in planta or in vivo, and in the case of *X. campestris* pv. *vesicatoria* and *X. euvesicatoria* pv. *allii*, which cause bacterial spot and leaf blight on tomatoes and onions, respectively, field experiments show that the efficiency was comparable to the application of copper-mancozeb treatments. Efficient control of bacterial pathogens and decrease in disease severity was also determined against soft-root bacteria, *Dickeya solani* and *Streptomyces scabiei*, on potatoes and radishes, respectively, *X. fastidiosa* on grapevines and olives, *R. solanacearum* on tomatoes, *P. carotovorum* subsp. *carotovorum* on lettuce, *X. axonopodis* pv. *citri* on grapefruit, *X. axonopodis* pv. *citrumelo* on oranges, *Pseudomonas tolaasii* on mushrooms and *E. amylovora* on pear and apple trees [57,58].

### 2.3. Advantages and Disadvantages of Antagonistic Microorganisms in Plant Protection

The utilization of antagonistic bacteria as biopesticides offers promising prospects for sustainable plant protection strategies. By incorporating these bacteria into pesticide formulations such as sprays, dusts and granules, effective pest management can be achieved while simultaneously promoting plant health and natural resistance mechanisms. Ongoing research endeavours to explore the full potential of biopesticide bacteria in agricultural practices. However, it is worth noting that the production of preparations based on *Pseudomonas* species is limited by a lack of spore production, which challenges formulation preparation and long-term storage [36]. Overcoming this problem and developing suitable formulations for *Pseudomonas* species is crucial to ensure their viability and efficacy as biopesticides over extended periods of time. It is also important to consider the diversity of species and how they influence certain properties of the host plant. Using multiple species in preparations broadens its action spectrum [45], but it also lengthens the registration process that entails seven steps, namely: isolation of microorganisms, characterization; determination of efficacy under controlled conditions; determination of efficacy under semi-controlled conditions; determination of efficacy in the field; standardization of the product and production; and, ultimately, production of a commercial biopreparation and launching the preparation on the market. On the other hand, biopesticides also can be less effective than chemical pesticides, and their effectiveness can be strongly affected by environmental factors such as temperature, humidity and soil pH [36]. The application of beneficial bacteria in field conditions is also one of the limiting factors, in terms of the complexity of research which entails interaction studies between various environmental factors and different genotypes of bacteria and other organisms [59]. For example, in contrast to the study by Krid et al. [53], the study by Ahmed and Hasnain [60] determined the negative impact of high temperatures on the survival of beneficial bacteria of the genus *Bacillus*. Furthermore, it is important to investigate the competitiveness of biopesticidal strains such as *Bacillus* spp. against the non-pathogenic strain of *Pantoea agglomerans*, which showed a suppressive effect against *P. syringae* in a recent study [55]. On the other hand, there are cases where mutualistic bacterial species can contribute to the spread and severity of diseases. This phenomenon often occurs between two or more bacterial species. For example, in the case of olive knot disease and in contrast to results obtained in the study by Broniarek-Niemiec et al. [55], the severity of the disease can be increased by the presence of non-pathogenic endophytic bacteria such as *P. agglomerans* and *Erwinia toletana* [61,62]. Therefore, the possibility of cooperation or coinfection between pathogenic and non-pathogenic bacteria should be considered as a significant factor in disease management approaches. Although the mechanisms of action of various antagonistic microorganisms are well studied [36,56,63], ongoing research aims to further explore the optimization and utilization of these biopesticidal bacteria to enhance plant health and reduce the reliance on conventional chemical pesticides.

## 3. Antibacterial Activity of Some Plant Waste Products

### 3.1. Importance of Management of Agricultural Byproducts and Wastes

In agriculture, the generation of byproducts and wastes is inevitable, and their improper disposal represents a major source of pollution to soil and groundwater. Although this is a global problem, the implementation of sustainable and circular economy practices for managing agricultural waste is poor or lacking. These wastes mainly originate from four major sectors, including livestock manure, byproducts, fruit and vegetable residues and crop residues. Exploring the potential uses of agricultural by-products and wastes not only addresses the issue of pollution but also opens opportunities for potential applications in various disciplines. The potential use and environmental management perspectives of these agricultural wastes have recently been comprehensively discussed [64,65]. From an environmental management standpoint, these waste materials can be harnessed for their value in areas such as bioenergy production, organic fertilizer production, soil amendment and bioremediation. Furthermore, agricultural wastes are generally rich in phenolic

content and therefore present a new source of substances that can be used to develop biopesticides [30,64–79].

### 3.2. Antibacterial Properties of Olive Mill Wastewater

Olive mill wastewater (OMWW), also known as olive mill effluent (OME), is recognized as one of the by-products that are characterized by its bioactivity and high content of phenolic compounds such as hydroxytyrosol glucoside, hydroxytyrosol, tyrosol, caffeic acid, verbascoside, oleuropein, luteolin, quercetin, apigenin, rutin and EDA-like components [67,68]. However, the management of OMWW presents a challenge in olive-growing regions due to its large volume, resulting in water and soil pollution caused by the concentrated phenolics [68]. Therefore, it is necessary to control waste disposal and utilize OMWW in sustainable ways. The amount of phenolic compounds can be influenced by storage conditions and duration. Proper storage and handling of OMWW are essential to preserve the phenolic content and maximize its future applications. For example, Feki et al. [69] observed that storing OMWW at 25 °C in the dark for five months resulted in a decrease in the amount of most phenolic compounds, while the amount of hydroxytyrosol increased. Further studies would need to explore the optimal storage conditions and duration to maintain the desired phenolic composition and bioactivity of OMWW. Despite the potential risks associated with its disposal, OMWW has shown promising results as an antimicrobial agent in some studies. Direct use of OMWW in its raw form is not recommended as it is toxic to humans, animals and the environment [70]. However, studies have also shown that even low concentrations of bioactive compounds can inhibit the growth of bacteria in laboratory experiments with its effect surpassing copper treatment [71]. For instance, OMWW has exhibited bactericidal effects on species such as *P. savastanoi* pv. *savastanoi* and *C. michiganensis*, using the original concentrations of polyphenols present in the wastewater [72]. Another study demonstrated the bactericidal activity of OMWW obtained from the Leccino olive cultivar against the seed-borne bacterium *X. campestris*, without interfering with seed germination. The MIC of total polyphenols was determined to be 2500 µg/mL for *X. campestris*. It was proposed that the bactericidal activity was a result of the interaction between polyphenols and bacterial proteins, leading to protein denaturation [73]. It is worth noting that the phenol oleuropein only inhibited the growth of the Gram-positive bacterium *B. subtilis*, suggesting that the concentrations of certain phenolic compounds may affect beneficial organisms present in/on plant hosts. Therefore, the extraction of individual compounds should be considered as an optimal solution to preserve non-pathogenic organisms and the biodiversity of microorganisms associated with various plant species. Furthermore, different olive cultivars were found to significantly differ in their total phenolic content, indicating that the antimicrobial activity among extracts may vary. Extracts obtained from cvs. Frantoio, Mission, Taggiasca and Picual were effective against some foodborne bacteria, including *Staphylococcus aureus*, *Escherichia coli*, *P. aeruginosa* and *Listeria monocytogenes* [74,75]. In a study by Krid et al. [71], the application of phenolic extracts from OMWW, which contained high concentrations of hydroxytyrosol, 3,4-dihydroxy phenylethanol (tyrosol), catechol, para-coumaric acid and caffeic acid, against *P. savastanoi* pv. *savastanoi* inhibited the formation of knots in olive plants (cv. Chemlali) significantly stronger than treatment with a copper-based preparation. Copper sulphate (0.5%) inhibited the weight of knots by around 50%. The effectiveness of extracts was attributed to the high concentrations of hydroxytyrosol. In contrast to these results, the study by Medina et al. [76] determined the antibacterial properties of numerous polymeric fractions against bacterial strains belonging to the genera *Erwinia*, *Pseudomonas* and *Clavibacter*. Briefly, the results showed that the antibacterial effect is likely the result of synergy among ingredients. For example, the ethyl acetate extract of wastewater showed significant inhibition of *P. savastanoi* and *E. amylovora* growth at concentrations ranging from 5 to 20%, respectively, while the wastewater itself exhibited MIC at concentrations from 10 to 20%, depending on the targeted bacterial species.

### Antibacterial Properties of Phenolic Compound Hydroxytyrosol

Hydroxytyrosol (HTyr) is a promising low molecular weight phenol found in OMWW, as well as in olive oil and olive leaves. It has antimicrobial activity against bacterial species such as *R. radiobacter* and *P. savastanoi* pv. *savastanoi*, which are known to induce tumors in plants [77]. Strong bactericidal activity has been observed with the application of hydroxytyrosol alone, as well as in its enriched form within OMWW extract. However, when hydroxytyrosol was used alone, even at its highest concentration (32.83 mg/g) it exhibited the weakest inhibition of both bacteria. Similar results were obtained by Medina et al. [76], where hydroxytyrosol alone did not show any antibacterial properties when used against *P. savastanoi*, whilst the antibacterial potential was determined against *E. amylovora* only at a concentration of 6.6 mmol/L. A greater inhibition of both bacteria was achieved with the hydroxytyrosol-enriched extract at its highest concentration (30.4 mg/mL). The effectiveness of both treatments was found to be concentration dependent, with lower concentrations showing decreased antibacterial activity. The strong bactericidal potential of OMWW extract is presumed to be the result of the synergy among different phenolic compounds present alongside HTyr. However, the cost of hydroxytyrosol remains a major disadvantage, and it is not clear if the efficiency of its use justifies the expense. Nonetheless, due to the estimated non-toxic properties of HTyr, it is considered an interesting molecule in the development of environmentally friendly pesticides for the future.

### 3.3. Other Agricultural and Agro-Industrial By-Products and Wastes Showing Antibacterial Properties

In addition to olive wastes, the studies listed in Table 1 investigated the antibacterial potential of various agricultural residues, pest plants, solid wastes and food industry by-products against economically important phytopathogenic bacterial species. Generally, the antibacterial properties against Gram-negative bacteria were relatively weaker, requiring higher concentrations (>1000 µg/mL) of the antimicrobials compared with the Gram-positive bacteria. In the study by Ditsawanon et al. [78], the antibacterial efficacy of hydrolates derived from agricultural waste products was comprehensively studied. The research focused on the antibacterial potential of hydrolates obtained from selected agricultural waste materials, including bagasse and rice straw, and agro-industrial residues such as coconut residue from coconut milk production and peanut seed coat from peanut-based snack production. The results indicated significant inhibition of growth among specific phytopathogenic bacterial species (Table 1). Remarkably, the utilization of purified protein hydrolate extracted from bagasse—an ATP-binding cassette domain-containing protein—exhibited a distinct mechanism of action compared with other studied peptides. For instance, an unidentified peptide and expansin were observed to impact the integrity of the cell wall membrane. In contrast, the ATP-binding cassette domain-containing protein demonstrated a different mechanism, targeting intercellular biological processes. The findings of this study underscore the potential significance of peptides for agricultural applications, particularly in managing phytopathogenic bacteria. Importantly, ATP-binding cassette domain-containing protein did not inhibit the growth of beneficial bacterial species *B. subtilis* and *P. fluorescens* in vitro. However, it did inhibit the growth of *Pectobacterium carotovorum*, implying its potential for targeted control.

**Table 1.** List of plant wastes tested for the antibacterial potential expressed as minimal inhibitory concentration (MIC) values against various plant pathogenic bacterial species used in different studies.

Reference Source	Bacterial Species	Plant Waste/By-Products	MIC	Determination Method	Mode of Action	
[73]	Ciafardini and Zullo	<i>Xanthomonas campestris</i>	OMWW phenols–cv. Leccino	2500 µg/mL	Agar diffusion	protein cross-linking and protein-denaturation



Table 1. Cont.

Reference	Source	Bacterial Species	Plant Waste/By-Products	MIC	Determination Method	Mode of Action
[72]	Capasso et al.	<i>Pseudomonas syringae</i> pv. <i>savastanoi</i> <i>Clavibacter michiganensis</i>	OMWW polyphenols and related compounds	$5 \times 10^{-4}$ mol/L	Broth dilution	damage to cell membrane
[76]	Medina et al.	<i>Erwinia uredovora</i> <i>E. toletana</i> <i>E. amylovora</i> <i>P. savastanoi</i> <i>P. syringae</i> <i>C. michiganensis</i>	Olive wastewater of stored semisolid olive residue	10–20% (v/v)	Broth dilution	n.t.
[77]	Pannucci et al.	<i>P. savastanoi</i> pv. <i>savastanoi</i> <i>Rhizobium radiobacter</i>	Hydroxytyrosol–HTyr Hydroxytyrosol enriched extract of OMWW–HTE	100–300 300–500 µg/mL	Disc diffusion Subculture method	n.t.
[79]	Chicchio et al.	<i>P. syringae</i> pv. <i>syringae</i> C. <i>michiganensis</i> subsp. <i>nebraskense</i>	Methanolic extracts of wastes/by-products: <i>Abutilon theophrasti</i> Medik. <i>Achillea millefolium</i> L. <i>Allium cepa</i> L. <i>Artemisia absinthium</i> L. <i>Beta vulgaris</i> L. <i>Camelina sativa</i> (L.) Crantz <i>Castanea sativa</i> Mill. <i>Cicer arietinum</i> L. <i>Cichorium intybus</i> L. <i>Cucurbita pepo</i> L. <i>Cupressus sempervirens</i> L. <i>Echinochloa crus-galli</i> (L.) P. Beauv. <i>Erigeron canadensis</i> L. <i>Helianthis annuus</i> L. <i>Laurus nobilis</i> L. <i>Lavandula angustifolia</i> Mill. <i>Melissa officinalis</i> L. <i>Origanum vulgare</i> L. <i>Phaseolus vulgaris</i> L. <i>Prunus amygdalus</i> Batsch <i>Rosa damascena</i> <i>Solanum lycopersicum</i> L. <i>Solanum tuberosum</i> L. <i>Sorghum bicolor</i> (L.) Moench <i>Thymus vulgaris</i> L. <i>Triticum aestivum</i> L. <i>Vitis vinifera</i> L.	>1000 µg/mL	Broth microdilution	n.t.
			<i>Helichrysum italicum</i> (Roth) G. Don	125–>1000 µg/mL		n.t.
			<i>Salvia officinalis</i> L. <i>Salvia rosmarinus</i> Schleid.	500–>1000 µg/mL		n.t.
			<i>Salvia sclarea</i> L.	1000–>1000 µg/mL		n.t.
[78]	Ditsawanon et al.	<i>X. oryzae</i> pv. <i>oryzae</i> <i>X. citri</i> <i>Pectobacterium carotovorum</i> <i>R. rhizogenes</i>	Agricultural waste (rice, corn, sugarcane, bagasse) Agro-industrial waste (soybean, peanut, coconut, coffee, fish)	§	Broth dilution	Disruption of cell wall membrane and intercellular biological processes

§ protein hydrolites and small peptides; n.t.—not tested.

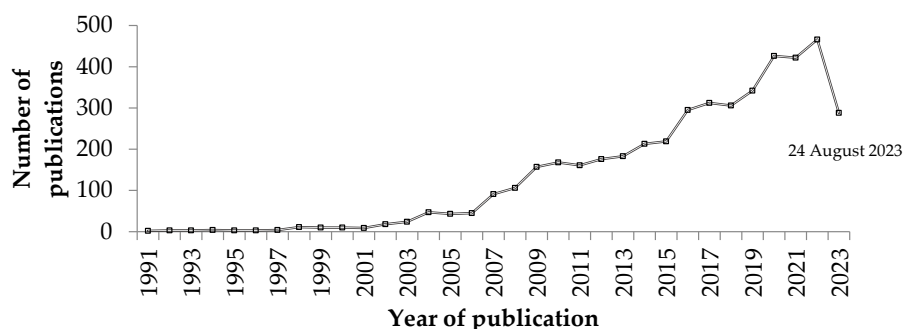
The antimicrobial potential of various plant by-products was tested in a recent study [79]. Tested by-products (Table 1), obtained from different parts and processes of cultivated and weed species, exhibited selective antibacterial properties. In particular, the efficacy of

selected treatments was strong against the Gram-positive species *C. michiganensis* subsp. *nebraskensis*. The antibacterial potential was determined for the solid waste derived from the distillation of aerial parts of three species within the *Salvia* genus. The key bioactive compound that was determined as the molecule of interest was rosmarinic acid. In contrast, treatments poorly affected the growth of Gram-negative species *P. syringae* pv. *syringae*. These findings highlight the challenging identification of effective antibacterial agents against Gram-negative bacterial strains.

Interestingly, fruit peels, commonly generated as household waste, have been studied for their antibacterial effects [80]. Some examples of potential antibacterial agents from fruit peels mentioned in the literature include peanut shells [81], pomegranate peel [82] and mandarin peel [83]. Other potential antimicrobials, such as jaboticaba (*Myrciaria cauliflora*) peel, grape (*Vitis* sp.) pomace, peels and seeds, as well as prickly pear (*Opuntia ficus-indica*) wastes, have been highlighted in studies focusing on their activity against human pathogenic bacteria [30]. These studies examined the antibacterial properties of extract and found it to be effective against various pathogenic bacteria such as *Klebsiella pneumoniae*. While studies did not specifically focus on plant pathogens, they suggest the investigated extracts could act as antibacterial agents for plant diseases as well. Jaboticaba, known for its anthocyanin-rich fruit peel, possesses compounds that exhibit antimicrobial activity. Similarly, grape pomace, peels and seeds contain bioactive compounds, including phenolics, flavonoids and tannins, which exhibit antimicrobial properties. Additionally, prickly pear extracts have shown antimicrobial activity against human pathogens. These extracts contain bioactive compounds, including phenolic compounds, which also may have potential applications in plant disease management, although more research is needed to explore their specific effects on plant-associated microorganisms.

#### 4. Antibacterial Activity of Essential Oils and Plants Extracts

The urge to implement a new approach to controlling bacterial diseases is demonstrated by a total of 4570 scientific papers indexed in the Web of Science Core Collection, searched using the keywords “essential oil” and “plant bacteria” (Figure 1).



**Figure 1.** Graphical presentation of increasing trend of scientific research focusing on the use of essential oils and their ingredients against various bacterial species based on data from Web of Science Core Collection using the keywords “essential oil” and “plant bacteria”. Available online: <https://www.webofscience.com/wos/woscc/summary/e9e2769f-ace1-4e30-9da4-9daffa8c0efa-9f82a284/relevance/1> (accessed on 24 August 2023).

These papers discuss the antibacterial efficacy of numerous essential oils (EOs) against various plant, human and foodborne pathogenic bacteria. The research on this topic can be traced back to 1991, with an initial publication rate ranging from 2 to 18 papers per year until the early 2000s. However, since 2013, there has been a significant intensification of research efforts, resulting in a considerable increase in the number of published papers. In the past decade (2014 to present), there has been a consistent growth in research activity, with over 200 papers published annually. Over the last five years, the number of publications per year has ranged from 312 to 466, indicating a substantial interest and engagement

in investigating the antibacterial properties of EOs. Notably, more than 50% of the listed papers were published between 2017 and 2023, indicating a recent surge in research focusing on this area. Plant extracts, particularly EOs, are known to encompass a diverse array of bioactive compounds, including phenolic compounds. These compounds offer potential alternatives for the control of phytopathogenic bacteria. Although the specific phenolic compositions may differ among plant extracts, they collectively contribute to the antimicrobial activity exhibited by these extracts. The increasing number of research papers in this field reflects the growing interest in seeking natural and environmentally friendly solutions for controlling bacterial pathogens.

#### 4.1. Antibacterial Potential of Essential Oils and Essential Oil Compounds

##### 4.1.1. Plant Species from the Lamiaceae Family

EOs have been investigated for their antimicrobial activity against a range of microorganisms, including fungi and human pathogenic bacteria, and as preservatives for fresh fruits [84–86]. EOs derived from plants are often readily accepted from a human perspective due to the traditional use of medicinal aromatic plants in many countries [87]. Chemical analyses of various plant species have revealed diverse plant metabolites, particularly high phenolic content, which have the potential for antimicrobial activity [88–90]. In addition to EOs, the most concentrated compounds that characterize the chemotypes of these oils are monoterpenoids and terpenoids with longer chains, such as menthol, geraniol, thymol, eugenol, carvacrol and others. These compounds contribute to the chemotypes of various plant species, including *Citrus limon* (lemon), *Mentha × piperita* (peppermint), *Geranium* sp. (geranium), *Lavandula* sp. (lavandin) and *Cymbopogon citratus* (lemongrass), among others [91]. The presence of specific compounds in EOs is dependent on the plant species. Commonly detected compounds in EOs also include  $\alpha$ -phellandrene, limonene, d-limonene, carvacrol, thymol,  $\alpha,\beta$ -thujone, camphor, carvone, menthol and menthone [92]. Some of these compounds have been shown to exhibit antimicrobial efficacy. Further research and exploration of the antimicrobial properties of these plant metabolites, both individually and in combination, can provide valuable insights into their potential applications in agriculture and plant disease management (Table 2). Notably, among the plant pathogenic bacteria, EOs derived from *M. piperita* (peppermint) have been frequently tested and shown antimicrobial potential. The use of EOs derived from *Mentha* plant species is expected to be more prevalent due to the presence of a high number of different species and cultivars within this genus. Studies suggest that various *Mentha* species are characterized by a high content of organic compounds with determined antibacterial activity, particularly phenols (terpenoids) such as eucalyptol, limonene, linalool, menthone, menthol, pulegone, linalyl acetate, carvone D, and more [90]. Nevertheless, the antibacterial potential of EOs is largely attributed to the synergy of various volatile compounds, rather than one specific compound [93,94]. According to the literature review by Wińska et al. [29], the EOs derived from *Mentha* species exhibit low antibacterial efficacy, except if the menthol is highly concentrated in oils. However, it is proposed that the *Mentha* EO can be used in combination with other EOs to induce higher sensitivity of bacteria to some antibiotics [95]. In the same study, carvacrol–thymol chemotypes of EOs of *Thymus* and *Origanum* species are highlighted. Moreover, combinations or synergistic effects of EOs, such as those derived from *Thymus* and *Origanum* species, have been found to exhibit antibacterial properties when applied undiluted, with higher susceptibility determined for *Xanthomonas* strains compared with *Pseudomonas* or *Erwinia* taxa [96]. Particularly low MIC values listed in Table 2, indicate high efficacy of *Thymus* and *Origanum* EOs as antimicrobials [96–102]. In the study by Bozkurt et al. [98], as well as previous studies, the EOs derived from *Thymus* and *Origanum* species, which are primarily composed of thymol and carvacrol, demonstrated the strongest inhibition of bacterial growth *in vitro*. Interestingly, the bioactivity against *P. savastanoi* pv. *savastanoi* was significantly greater compared with *P. savastanoi* pv. *nerii*, which are closely related pathogens known to induce tumors in host plants. The carvacrol chemotype *Origanum* EO was the most efficient antibacterial in the study by

Todorović et al. [103], where the lowest MIC values (0.02–0.32 µg/mL) were determined against *Pseudomonas*, *Xanthomonas* and *Clavibacter* strains. Other EOs obtained from plants belonging to *Lavandula*, *Citrus* and *Salvia* taxa were effective at concentrations > 0.32 µg/mL. However, there are contrary observations in the literature, where the EO obtained from *Satureja hortensis* (summer savory), characterized by high concentrations of carvacrol (79.17%), showed lower antibacterial potential compared with the EO of *Calamintha nepeta* (calamint) with the highest concentrations of cis-Piperitone epoxide (48.66%) [104]. Generally, it was determined in in vitro studies that the application of EOs exhibits higher MIC values against species belonging to *Pseudomonas* genera than those belonging to *Erwinia*, *Ralstonia*, *Xanthomonas*, *Clavibacter*, etc. [96,102–104]. These findings suggest further investigation of specific biological mechanisms that may differentiate these species. Also, the observed variability in antibacterial activity highlights the complexity of interactions between EOs and bacterial strains within the *Pseudomonas syringae* complex. A lower efficiency against *P. savastanoi* compared with *R. radiobacter* was observed in the study by Caparrotta et al. [93], suggesting that susceptibility to the same concentrations of plant-based compounds, e.g., EOs, can significantly vary among targeted strains. Further, the EOs derived from basil, sage, rosemary and marjoram have shown relatively lower effectiveness against Gram-negative *Pseudomonas* and *Xylella* species, for example [97,105]. Specifically, the MIC of *Salvia sclarea* (clary sage) against *X. fastidiosa* was 500 µg/mL, because of which it is categorized as a weak antimicrobial [97]. Nonetheless, EOs from sage (*Salvia*) species are enumerated as promising antibacterial compounds as alternative antimicrobials due to determined antibacterial potential depending on specific plant species, suggesting that further evaluation and development of biopesticides derived from *Salvia* species may be worth exploring. Importantly, the plant's chemical profile highly depends on genetics, climate and cultivation practice, thus suggesting the optimization of cultivation and identifying the most promising cultivar for further evaluation of less effective EOs, which could potentially act in synergy with some conventional pesticides or antibiotics. The oils from plant species belonging to the *Lavandula* genus can reduce antibiotic resistance of numerous human pathogenic bacterial species [106].

Of interest, *O. vulgare* (oregano) EOs were non-toxic to human neuroblastoma cell lines (IC<sub>50</sub> = 50.5 µg/mL) [99], and therefore could be considered as safe compound for further evaluation for control of bacterial diseases in agriculture. However, it is important to mention that EOs and their compounds can exhibit phytotoxic effects on plant hosts [107], which highly depends on used concentrations [99,107]. Hence, future studies need to evaluate the phytotoxic effect of potential antibacterials to avoid damage to plants in the field. Also, studies warrant the investigation of combinations of some EOs to expand the spectrum of potential plant protection preparations, due to documented interaction between plant species—bacterial species—compound.

#### 4.1.2. Plant Species Other Than Lamiaceae

Outside of the well-studied species of Lamiaceae, EOs derived from olive, almond and neem have demonstrated high efficacy against some human pathogens and could be potential pesticide candidates against plant pathogenic bacteria [108]. In the study by Sánchez-Hernández et al. [109], it was determined that *Ginkgo biloba* (ginkgo) EO exhibited strong antibacterial activity. At a concentration of 2 times MIC (1000 and 1500 µL/mL), the EO completely inhibited infection of *C. michiganensis* subsp. *michiganensis* in tomato plants and *P. syringae* pv. *pisi* in pea plants. Remarkably, no phytotoxicity was observed in any of the treatment groups, indicating the safety of *G. biloba* leaf extract as a natural pesticide. In the study by Tarakanov and Dzhililov [100], two EOs obtained from *Cinnamomum cassia* (Chinese cinnamon) and *O. vulgare* (oregano), inhibited the growth of *P. savastanoi* pv. *glycinea* and *Curtobacterium flaccumfaciens* pv. *flaccumfaciens* in vitro and in vivo at MIC of 200 and 1600 µg/mL, respectively. In foliar treatments or direct application on infected seeds at their MBC values, the inhibition of disease severity was more than 50%, without phytotoxicity. The antibacterial properties of cinnamon and oregano EOs were attributed

to the presence of cinnamaldehyde and carvacrol compounds. Specifically, these EO treatments were found to be more effective than the standard fungicide–bactericide Kocide. It is worth noting that the phytotoxicity of the applied treatments *in vivo* followed a dose-dependent pattern, with a safe threshold of 0.5% solution of EOs, below which no adverse effects on plant health were observed. Another study [2] determined the antibacterial potential of the EO of *Tagetes minuta* (khaki weed). This EO showed remarkable inhibitory activity against *Xanthomonas* and *Pseudomonas* bacteria at higher concentrations of treatment. Interestingly, the MIC value was lower for the *Pseudomonas* strain compared with *Xanthomonas*, indicating higher sensitivity of *Pseudomonas* to this EO. Furthermore, the EO of *T. minuta* exhibited stronger activity compared with the standard broad-spectrum bactericide Enrich BM (immunomodulator 2-bromo-2-nitropropane 1,3 diol). Minimal bactericidal concentrations of 950 µg/mL were determined for *X. axonopodis* pv. *phaseoli* (causal agent of bean blight) and *P. savastanoi* pv. *phaseolicola* (causal agent of halo blight of beans), while a bactericidal concentration of 1900 µg/mL was determined for *X. axonopodis* pv. *manihotis* (causal agent of cassava bacterial blight). Overall, all tested Gram-negative bacterial strains exhibited high sensitivity to the application of *T. minuta* crude oil. The antibacterial effectiveness of *T. minuta* EO is attributed to its high concentrations of monoterpenes and sesquiterpenes. Moreover, prolonged incubation of bacteria (48 h) further enhanced the inhibitory effect against *Pseudomonas* bacteria. These findings suggest that *T. minuta* EO possesses potent antibacterial properties, particularly against troublesome *Pseudomonas* strains, which is interesting since in the literature, the strongest antibacterial effect of plant compounds is often reported against Gram-positive strains. Moreover, the application of *Laurus nobilis* L. (bay laurel) EO showed interesting results [110]. Specifically, the undiluted EO was more selective towards *P. syringae* pv. *phaseolicola*, with less antibacterial effect against the Gram-positive *B. subtilis*.

In addition to *Xanthomonas* species, the EO of *Citrus aurantium* (sour orange) and *Cymbopogon winterianus* (lemongrass) were effective against *X. citri* subsp. *citri* with MIC values of 0.238 and 0.121 µL/mL, compared with *Foeniculum vulgare* (fennel), *Pinus eliotii* (pine) and *Ocimum gratissimum* (basil) with MIC of 1.81, 7.81 and 0.43 µL/mL [94]. Also, Janačković et al. [111] determined that the EO extracted from flowering *Ambrosia artemisiifolia* (common ragweed) exhibited pronounced activity against several strains of Gram-negative phytopathogenic bacteria listed in Table 2. This finding suggests the potential use of this allergenic weed species and its EO in the control of plant diseases. The study highlights the possibility of utilizing natural resources, such as weed species, as a source of bioactive compounds. Similarly, in a study by Boučekouk et al. [112], the EO obtained from *Pteridium aquilinum* (bracken fern) demonstrated high potency against three economically important phytopathogenic bacteria. This EO was characterized by a high concentration of the compound linalool. These results support the previous literature reports on the potential of linalool as a molecule of interest for the control of bacterial diseases. Regarding individual molecules, the terpenes (p-cymene, γ-terpinene and limonene) exhibit lower or no antimicrobial efficiency [113]. However, p-cymene can enhance the antimicrobial potential of certain terpenoids, such as carvacrol, by affecting bacterial membranes and flagellar movement [105]. Another group of compounds, phenylpropenes, including eugenol, vanillin and cinnamaldehyde, have shown notable antibacterial activity against Gram-negative bacteria, with isoeugenol and eugenol exhibiting greater efficacy [114].

Promising EO against *Rhizobium radiobacter* and *E. carotovora* var. *carotovora* was derived from *Thuja occidentalis* (white cedar) exhibiting lower MIC values (400 and 350 mg/L), compared with other 17 EOs tested [115]. Nevertheless, most EOs in the same study showed similar MIC values against both bacterial strains, while the EO of *Myrtus communis* (common myrtle) was defined as weak antimicrobial (MIC > 1000 µg/mL). Notably, it is demonstrated that the EOs with diverse compounds in their chemical profile, showed stronger inhibition of bacterial growth. Specifically, in a study by Feizi et al. [116], the EO of *Ziziphora clinopodioides* showed greater antibacterial properties with a MIC value of 6 µL/mL against *P. syringae* pv. *syringae* compared with thymol chemotype *Carum capticum*

EO with a MIC of 18  $\mu\text{L}/\text{mL}$ . The effectiveness of these EOs is attributed to the synergy of compounds in their chemical profile. Conversely, [94] a stronger antibacterial effect was determined for EOs that have a simple composition. Overall, these contradicting observations warrant further investigation of individual compounds alone or in mixtures to confirm which compounds could act in synergy or interact as antagonists.

Further, *Amyris balsamifera* (Indian sandalwood) and *Pogostemon patchouli* (patchouli) EOs showed activity against *X. fastidiosa*, with inhibition of biofilm formation by 50% using concentrations of 250 and 125  $\mu\text{g}/\text{mL}$ , suggesting their moderate antibacterial potential [97]. The most concentrated compounds of these EOs were  $\alpha$ -Gurjuene and  $\gamma$ -eudesmol. Even though the bacterial biofilm is less sensitive to antimicrobials, its inhibition by 50% suggests further research targeting other bacterial species. For this, further research on the mode of action is necessary. An additional suggestion is testing compounds in mixtures/combinations to broaden the spectrum and the mode of action as suggested by Patel et al. [102]. For example, a compound that disrupts cell membranes could allow better penetration of compounds that interfere with intercellular processes in bacterial cells.

#### 4.2. Antibacterial Properties of Plant Extracts

Generally, EOs show higher inhibition of bacterial growth compared with plant extracts. In the case of *C. michiganensis* subsp. *michiganensis*, the antibacterial activity of pure *M. suaveolens* (apple mint) and *C. ladaniferus* (gum rockrose) EOs was slightly higher than treatment with antibiotics [87]. However, EOs inhibited the germination of tomato seeds, while the plant extracts were less effective but did not significantly reduce germination. Inhibition of seed germination by application of EOs contradicts the previously mentioned use of OMWWs as antimicrobials against *C. michiganensis* species [71]. It is proposed that the inhibition of germination might be attributed to allelopathy [87]. Overall, it is concluded that methanolic plant extracts of *C. ladaniferus* can be used as an alternative control measure against *C. michiganensis* on tomato seeds without interfering with germination, despite their lower total phenolic content. The antibacterial activity of the plant extracts of *C. ladaniferus* is attributed to the presence of sesquiterpenoid viridiflorol, which has been previously suggested as a safe natural pesticide in agriculture [117].

In the study by Fontana et al. [118], the efficacy of leaf extracts from *Moringa oleifera* (moringa) was evaluated against *E. amylovora*, the causal agent of fire blight in apple and pear trees. Application of leaf extracts significantly reduced the symptoms of infection, particularly when the treatments were applied prior to the onset of infection on apple shoots. This finding suggests the potential use of *M. oleifera* as a natural alternative for the management of fire blight disease. By reducing the symptoms of infection, these extracts have the potential to contribute to the protection and health of widely cultivated apple trees. In another study, a crude extract obtained from *Annona atemoya* (atemoya), which was characterized by a high concentration of the phytochemical rutin, demonstrated strong activity against the gall-forming bacterium *R. radiobacter* [119]. In another study [100], a strong antibacterial effect was determined using ethanolic extract of *Bergenia crassifolia* (leather bergenia) against two economically important pathogens of soybean—*P. savastanoi* pv. *glycinea* and *C. flaccumfaciens* pv. *flaccumfaciens*. The antibacterial effect was attributed to the presence of 5-Methyl-3-methylenedihydro-2(3H)-furanone. A MIC of 1000 to 2500  $\mu\text{g}/\text{mL}$  was determined against both bacteria, with lower values determined against *P. savastanoi* pv. *glycinea*. Although the plant compounds are often phytotoxic, when these treatments were applied in vivo using 0.5% solution of EOs and 13% of plant extracts, no damage was observed on plants. In addition, these results confirm the strong activity of EOs at low concentrations, thus suggesting their use as plant protection agents that could be implemented in formulations.

Moreover, the hydroalcoholic extract of *Larrea tridentata* (creosote bush) [120], showed a strong antibacterial effect against multidrug-resistant strains of *C. michiganensis* subsp. *michiganensis*, *P. syringae* and *X. campestris* in vitro. The MIC of extract alone, as well as the aqueous (LTAq-F) and organic fraction (LTeTOAc-F) of extract, ranged from 0.39

to 6.25 mg/mL. The lowest MIC and minimal bactericidal concentration (MBC) against targeted bacterial strains was lowest for *L. tridentata* organic fraction. Interestingly, the plant extract and organic fraction were bactericidal in nature, conversely to the application of the aqueous fraction. Also, the authors highlighted that the stronger efficiency of the organic fraction was due to a higher yield of bioactive compounds. The observed antibacterial activity was proposed to be influenced by the presence of lignans, which exhibit various mechanisms of action that can interfere with cell membranes and protein transport systems, leading to cell death. Also, it could be assumed that the antibacterial effect was influenced by the presence of the phenols thymol and carvacrol, as these compounds are constituents of numerous EOs and are often determined as the most efficient agents against pathogenic bacteria [120]. These findings highlight the potential use of an organic fraction of *L. tridentata* extract in the control of drug-resistant bacterial strains in agriculture. In the overall context of plant extract use, it is worth considering the extraction process type and solvent used, as alcoholic extracts often result in a stronger antibacterial effect than aqueous extracts.

#### 4.3. Mechanism of Action of Plant-Based Compounds against Gram-Positive and Gram-Negative Bacterial Species

The antibacterial activity of EOs is believed to be attributed to the synergy of various mechanisms that target bacterial cells, giving rise to what is known as the “essential oils versatility”. EOs can exert toxicity on bacterial cells by causing cell degradation, cytoplasmic coagulation, leakage of metabolites and ions from the cytoplasm, alterations in proton motive force and membrane fatty acids, increased membrane permeability, disruptions in intra- and extracellular ATP and ATPases, and distortions in membrane proteins. They can also interfere with anti-quorum sensing mechanisms, leading to a decrease in proteolytic activity, biofilm formation and inhibition of factors involved in bacterial virulence [105,121]. Hydrophobic chemical components found in EOs often exhibit lower antibacterial activity against Gram-negative bacteria compared with Gram-positive bacteria. This is due to the presence of a complex lipopolysaccharide outer membrane in Gram-negative bacteria, which can block or delay the penetration of EOs through the membrane [114]. However, it is important to note that the outer membrane of Gram-negative bacteria is not completely impermeable, allowing some penetration of hydrophobic molecules. In contrast, Gram-positive bacteria have a more permeable membrane to hydrophobic compounds, making them more sensitive to EO and plant extract application [105]. Additionally, EOs from plant species belonging to the Lamiaceae family have demonstrated strong antibacterial activity against plant pathogenic bacteria even at extremely low concentrations. The efficacy of treatments at lower concentrations is attributed to their impact on cellular enzymes, while higher concentrations can lead to protein denaturation [105]. It is important to note that the antimicrobial activity of EOs and plant extracts can vary depending on the specific bacterial strain, concentration, and composition of the oil, due to the variabilities in aromatic and phenolic profile which depends on climate, genetics, environment and agricultural practice [118,122]. The mode of action of EO components is highly dependent on the specific position of functional groups within their molecular structures, such as hydroxyl and alkyl groups. Additionally, the effectiveness of EOs can vary among different bacterial strains, highlighting the importance of investigating the virulence and pathogenicity of individual strains for effective management. This variability is exemplified in a study conducted by Hsouna et al. [123], where the antibacterial properties of the menthol chemotype of *M. piperita* EO exhibited significant variations in efficiency against different strains of *R. radiobacter* (with MIC ranging from 10 to 12,500 µg/mL). The study also confirmed that the mechanism of action of *Mentha* EO involved the disruption of the bacterial membrane, even at concentrations as low as half of the MIC. Furthermore, in vivo application of *Mentha* EO resulted in complete prevention of disease occurrence in tomato plants inoculated with *R. radiobacter*.





Table 2. Cont.

Reference	Source	Bacterial Species	Plant Species	MIC	Determination Method	Mode of Action
[123]	Hsouna et al.	<i>R. radiobacter</i>	<i>Mentha piperita</i> L. EO	10–12,500 µg/mL	Disc diffusion Broth microdilution	Disruption of cell membrane
[119]	Al-Baharwee et al.	<i>R. radiobacter</i>	<i>Annona atemoya</i> Mabb.	15.6–31.3 µg/mL	Agar well diffusion Broth microdilution	Damage to cell membrane
[2]	Muthee-Gakuubi et al.	<i>Xanthomonas axonopodis</i> pv. <i>phaseolicola</i> <i>X. axonopodis</i> pv. <i>manihotis</i> <i>P. savastanoi</i> pv. <i>phaseolicola</i>	<i>Tagetes minuta</i> L. EO	12,000–48,000 µg/mL	Disc diffusion Broth dilution	n.t.
[87]	Benali et al.	<i>Clavibacter michiganensis</i> subsp. <i>michiganensis</i> <i>P. savastanoi</i> pv. <i>savastanoi</i>	<i>Mentha suaveolens</i> L., <i>Cistus ladanifer</i> L. EOs and methanolic and ethanolic extracts	190–780 µg/mL	Disc diffusion Broth microdilution	n.t.
[111]	Janačković et al.	<i>X. campestris</i> pv. <i>campestris</i> <i>Erwinia amylovora</i> <i>P. syringae</i> pv. <i>syringae</i> <i>X. arboricola</i> pv. <i>juglandis</i>	<i>Ambrosia artemisiifolia</i> Michx. L.EO	4–1,500,000 µg/mL	Broth microdilution	n.t.
[120]	Morales-Ubaldo et al.	<i>C. michiganensis</i> subsp. <i>michiganensis</i> <i>P. syringae</i> <i>X. campestris</i>	Hydroalcoholic extract <i>Larrea tridentata</i> (DC.) Coville	3120–8000 µg/mL	Disc diffusion Broth microdilution	Affect proteins of the ATP binding cassette transport system
[112]	Bouchekouk et al.	<i>E. amylovora</i> <i>P. carotovorum</i> subsp. <i>carotovorum</i> <i>P. savastanoi</i> pv. <i>savastanoi</i>	<i>Pteridium aquilinum</i> (L.) Kuhn EO	0.625–5.00 µL/mL	Disc diffusion Agar diffusion	n.t.
[99]	Grul'ová et al.	<i>C. michiganensis</i> <i>P. syringae</i> pv. <i>phaseolicola</i> <i>P. savastanoi</i> <i>X. campestris</i>	<i>Origanum vulgare</i> L. EO	100–10,000 µL/mL	Disc diffusion	n.t.
[93]	Caparrotta et al.	<i>R. radiobacter</i> <i>P. savastanoi</i> pv. <i>savastanoi</i>	<i>Boswellia papyrifera</i> (Delile ex Caill.) Hochst. <i>B. frereana</i> Birdw. <i>B. dalzielii</i> Hutch. <i>B. rivae</i> Engl. <i>B. neglecta</i> S.Moore <i>Canarium madagascariensis</i> Engl. <i>C. schweinfurtii</i> Engl. <i>Bursera bipinnata</i> (DC.) Engl. <i>B. microphylla</i> A.Gray <i>Commiphora guidotti</i> Chiov. <i>C. wildii</i> Merxm. <i>Hymenaea verrucosa</i> Gaertn. EOs	0.2% (v/v)	Overnight incubation in liquid medium without dilution	n.t.

Table 2. Cont.

Reference Source	Bacterial Species	Plant Species	MIC	Determination Method	Mode of Action	
[97]	Brentini Santiago et al.	<i>Xyllela fastidiosa</i>	<i>Pogostemon patchouli</i> Pellet. <i>Amyris balsamifera</i> L. <i>Cinnamomum zeylanicum</i> Blume <i>Cedrus atlantica</i> (Endl.) G.Manetti ex Carriere <i>Commiphora myrha</i> (T.Nees) Engl. <i>Cupressus sempervirens</i> L. <i>Citrus paradisi</i> Macfad. <i>Boswellia carterri</i> Flueck. <i>Citrus aurantium</i> L. <i>Salvia sclarea</i> L. <i>Thymus vulgaris</i>	125 µg/mL 500 µg/mL	Broth microdilution Microtitration plate assay	n.t.
		<i>Citrus bergamia</i> Risso & Poit. <i>Eucalyptus globulus</i> Labill. <i>Zingiber officinale</i> Roscoe <i>Cinnamomum camphora</i> (L.) J.Presl <i>Abies sibirica</i> Ledeb. <i>Melaleuca alternifolia</i> (Maiden & Betche) Cheel	1000 µg/mL			
[96]	Vasinauskiene et al.	<i>E. carotovora</i> subsp. <i>carotovora</i> <i>X. vesicatoria</i> <i>P. marginalis</i> pv. <i>marginalis</i> <i>P. syringae</i> pv. <i>syringae</i> <i>P. syringae</i> pv. <i>tomato</i> <i>Bacillus</i> sp.	<i>Origanum vulgare</i> <i>Acorus calamus</i> L. <i>Achillea millefolium</i> L. <i>Achillea filipendulina</i> Lam. <i>Achillea cartilaginea</i> Petri <i>Carum carvi</i> L. <i>Mentha piperita</i>	Undiluted	Disc diffusion	n.t.
[104]	Gormez et al.	<i>R. radiobacter</i> <i>Bacillus pumilus</i> <i>C. michiganensis</i> subsp. <i>michiganensis</i> <i>Enterobacter intermedius</i> <i>Erwinia carotovora</i> subsp. <i>carotovora</i> <i>E. chrysanthemi</i> <i>P. cichorii</i> <i>P. corrugate</i> <i>P. fluorescens</i> <i>P. syringae</i> pv. <i>syringae</i> <i>P. syringae</i> pv. <i>phaseolicola</i> <i>P. syringae</i> pv. <i>pisii</i> <i>P. syringae</i> pv. <i>tabaci</i> <i>P. syringae</i> pv. <i>tomato</i> <i>Ralstonia solanacearum</i> <i>X. campestris</i> pv. <i>campestris</i> <i>X. vesicatoria</i>	<i>Calamintha nepeta</i> (L.) Kuntze <i>Satureja hortensis</i> L.	7.81–31.25 µg/mL	Disc diffusion Broth dilution	n.t.

Table 2. Cont.

Reference	Source	Bacterial Species	Plant Species	MIC	Determination Method	Mode of Action
[116]	Feizi et al.	<i>P. syringae</i> pv. <i>syringae</i>	<i>Carum capticum</i> <i>Ziziphora clinopodioides</i> Lam.	Undiluted	Disc diffusion Well diffusion Vapor phase test	n.t.
[110]	Mamoucha et al.	<i>P. syringae</i> pv. <i>phaseolicola</i>	<i>Laurus nobilis</i> L.	Undiluted and 1.25% (v/v)	Disc diffusion Well diffusion	n.t.
[102]	Patel et al.	<i>P. cichorii</i> <i>P. syringae</i> <i>X. perforans</i>	<i>Nepeta cataria</i> L. <i>Origanum vulgare</i>	2.5–5.0 % (v/v)	Agar well diffusion	n.t.
[103]	Todorović et al.	<i>P. tolaasii</i> <i>C. michiganensis</i> subsp. <i>nichiganensis</i> <i>X. campestris</i> pv. <i>phaseoli</i>	<i>Illicium verum</i> Hooker <i>Juniperus oxycedrus</i> L. <i>Eucalyptus globulus</i> Labilardie <i>Lavandula angustifolia</i> Mill. Citrus lemon L. <i>Cymbopogon flexuosus</i> Stapf. <i>Mentha piperita</i> <i>Origanum vulgare</i> <i>Pinus nigra</i> L. <i>Pinus pinaster</i> Aiton <i>Pinus silvestris</i> L. <i>Rosmarinus officinalis</i> L. <i>Salvia officinalis</i> L. <i>Abies alba</i> Mill. <i>Gaultheria procumbens</i> L.	0.02–>32 µg/mL of air	Well diffusion (volatiles)	n.t.
[109]	Sánchez-Hernández et al.	<i>C. michiganensis</i> subsp. <i>michiganensis</i> <i>P. cichorii</i> <i>P. syringae</i> pv. <i>pisi</i> <i>P. syringae</i> pv. <i>syringae</i> <i>P. syringae</i> pv. <i>tomato</i> <i>X. vesicatoria</i>	Hydroalcoholic extract: <i>Ginkgo biloba</i> L.	500 µL/mL 750 µL/mL 750 µL/mL 750 µL/mL 1000 µL/mL	Agar dilution	n.t.
[115]	Badawy and Abdelgaleil	<i>R. radiobacter</i> <i>E. carotovora</i> subsp. <i>carotovora</i>	<i>Artemisia Judaica</i> L. <i>Artemisia monosperma</i> Delile <i>Callistemon viminalis</i> (Sol. ex Gaertn.) G.Don <i>Citrus aurantifolia</i> (Christm.) Swingle <i>Citrus lemon</i> <i>Citrus paradisi</i> <i>Citrus sinensis</i> (L.) Osbeck <i>Cupressus macrocarpa</i> Hartw. ex Gordon <i>Cupressus sempervirens</i> L. <i>Myrtus communis</i> L. <i>Origanum vulgare</i> <i>Pelargonium graveolens</i> L.'Her. <i>Rosmarinus officinalis</i> (L.) Schleid. <i>Syzygium cumini</i> (L.) Skeels <i>Schinus molle</i> L. <i>Schinus terebinthifolius</i> Raddi <i>Thuja occidentalis</i> L. <i>Vitex agnus-castus</i> L.	350–>1000 µg/mL	Broth dilution	n.t.

Table 2. Cont.

Reference Source	Bacterial Species	Plant Species	MIC	Determination Method	Mode of Action	
[94]	Sauer et al.	<i>X. citri</i> subsp. <i>citri</i>	<i>Citrus aurantium</i> L. <i>Cymbopogon winterianus</i> Jowitt <i>Foeniculum vulgare</i> Gaertn <i>Pinus elliottii</i> Engelm <i>Ocimum gratissimum</i> L.	0.121–7.81 µL/mL	Broth microdilution	n.t.

n.t.—not tested.

#### 4.4. Future Aspects of Potential Biopesticides in Agriculture

Stability and preservation are crucial in the practical application of biopesticides. To overcome the evaporative nature and enhance the stability of EOs, phenolic compounds and other plant-derived compounds, encapsulation in chitosan nanoparticles has been proposed as a promising solution for their application as antibacterial preparations in agriculture. Encapsulation ensures controlled release of the compounds over time and improves their stability by reducing evaporation and degradation [12,124,125]. Encapsulation has been found to reduce the MICs compared with the free forms of oils, indicating improved effectiveness [85,126]. The cost of extracting plant metabolites and the complexity of chemical synthesis present limitations to the widespread use of terpenoids and other plant compounds with antibacterial activity. Although the plant compounds are promising agents in the control of phytopathogenic bacteria, standardization of extraction is required with more studies to obtain reliable results across various agricultural and horticultural settings [77]. The extraction methods required for commercial production of plant extracts can be costly and demanding in terms of skilled personnel needed to obtain high-yield products [117]. However, due to the documented effectiveness of low concentrations of numerous bioactive compounds, it is possible to ensure preliminary low-cost preparations to determine their profitability in the agricultural economy.

## 5. Conclusions

Plant diseases cause significant yield losses in global plant production, which is a major concern considering the increasing human population and the demand for high-quality and high-yield food production. Also, farmers face challenges due to restrictions on the use of many active chemical compounds in plant protection. Public concerns about the toxicity of these compounds to the environment and human health have led to their limited use. Considering these demands, beneficial microorganisms show considerable prospects. The most promising results might be achieved by applying antagonist bacterial strains of the *Pseudomonas* and *Bacillus* genera. The advantage of microbial biopesticide use is its biodegradable nature and targeted action. In contrast, it is limited by the high cost of production, limited supply, slow action and reduced efficacy in field conditions. As an alternative, bacteriophages are emerging as effective antibacterials due to documented suppression of disease in in planta experiments, comparable to copper-based preparations. However, rapid evaluation of the resistance of phytopathogenic bacteria to bacteriophages has remained an important constraint.

Also, certain plant-derived compounds, such as hydroxytyrosol, have been determined to be safe for plants, supporting their potential use in agriculture. Furthermore, plant metabolites, particularly phenolic compounds present in EOs and plant extracts, exhibit significant antibacterial effects. The mechanism of action of EOs involves damaging bacterial cell membranes and interfering with essential cellular processes. The versatility of EOs is attributed to diversity in mode of action, often more potent against Gram-positive bacteria than Gram-negative. In general, EOs obtained from species belonging to the family Lamiaceae show the strongest potential as antibacterials. Purified EOs generally showed higher inhibition than plant extracts against numerous tested bacterial strains. When the use of plant extracts is considered, alcoholic extracts generally have a stronger effect than

aqueous extracts, which warrants further research to determine their effect on plants and their long-term effect on soil and the environment. All plant-based compounds need to be stabilized for storage when considering wider use. Innovative approaches such as microencapsulation of EOs in chitosan have shown promise in enhancing their inhibitory potential against bacteria, their stability and controlled release in agricultural applications, offering potential solutions for more targeted and efficient antimicrobial treatments. Also, it is important to consider that single concentrations of plant-based compounds will inhibit bacterial growth differently depending on species and even the pathovar.

Overall, this review underscores the importance of the development of novel techniques to enhance the efficacy of antimicrobial compounds in the control of bacterial diseases in plants. Although extraction and the synthesis of plant metabolites and compounds can be costly and complex, their potential as an alternative to managing bacterial diseases in agriculture is evident. With a significant portion of global plant production losses attributed to bacterial diseases, there is a pressing need for effective and environmentally friendly biopesticides. We believe that this approach can contribute to the development of more efficient and targeted antimicrobial treatments in the future. Further research and optimization of application methods are needed to help establish the practicality in the context of plant disease management strategies in field conditions.

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