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Review

Glycerol as an Inducer of Disease Resistance in Plants: A Systematic Review

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Abstract: The objective of this systematic review (SR) was to select studies on the activity of glycerol as a molecule that induces disease resistance in plants. We sought to evaluate articles deposited in five electronic databases using a search string and predefined inclusion and exclusion criteria. The most studied crops are *Arabidopsis thaliana*, *Glycine max*, and *Coffea* spp. The most commonly cited biotic agents include *Pseudomonas syringae*, *Blumeria graminis*, and *Colletotrichum higginsianum*. Numerous doses of glycerol were studied, and concentrations ranged from 0.004 to 9.21%, with a 3% concentration of glycerol being considered most effective for most plant species, where greater resistance was observed with increased glycerol-3-phosphate (G3P) and decreased oleic acid levels. The main means of application of the product were spraying and immersion. The SR also revealed the evaluation of resistance-inducing genes, such as *PR proteins* (*PR-1*, *PR2*, *PR-5*, etc.), *HPS70*, *HSP90*, *SCAM4*, and Tapr1, among others. The information collected in this SR helps to understand the state of the art on the use of glycerol as a molecule inducing resistance against biotic stressors to understand the mechanisms involved in most host–pathogen relationships. This information will be useful in plant breeding programs and for growers/producers.

Keywords: defense genes; disease resistance; glycerol-3-phosphate; oleic acid; PR proteins; signaling molecule

Citation: Novaes, A.P.d.S.; Nascimento, F.d.S.; Rocha, A.d.J.; Soares, J.M.d.S.; Ramos, A.P.d.S.; Junior, L.C.d.S.; Rodrigues, A.d.S.; Mendes, T.A.d.O.; Rocha, L.d.S.; Amorim, E.P.; et al. Glycerol as an Inducer of Disease Resistance in Plants: A Systematic Review. *Horticulturae* **2024**, *10*, 1368. https://doi.org/10.3390/horticulturae10121368

Academic Editor: Marc Chillet

Received: 30 September 2024
Revised: 14 November 2024
Accepted: 17 November 2024
Published: 20 December 2024

1. Introduction

The various diseases caused by viral, fungal, and bacterial pathogens compromise the development of plants, affecting their final productivity. Among these microorganisms, there are specific ones such as biotrophic microorganisms that depend on the living plant to feed and complete their life cycle; necrotrophs, which, during their feeding behavior, kill the host plant; and hemibiotrophic microorganisms, which initially rely on the living plant to survive and complete their cycle with a necrotrophic phase, where the host is degraded [1,2]. One characteristic that differentiates biotrophic fungi from the others is their reproductive difficulty in a laboratory setting in a nonliving environment [3].

Glycerol has been used to control plant diseases. It is an oil derived from epichlorohydrin, obtained from propylene. Plants are also used to produce glycerol, but it can also be obtained from petrochemical production [4,5]. Glycerol is considered an organic fungicide, and research results have determined that when used correctly, it helps with resistance to several fungal diseases [6]. It is believed that the glycerol signaling molecule in plants is glycerol-3-phosphate (G3P), which, together with the metabolism of primary carbohydrates, contributes to greater plant resistance to fungal attacks [7].

Plants can prevent pathogen attacks through induced systemic resistance (ISR) and systemic acquired resistance (SAR). What differentiates these is the type of induction in the plant. SAR is activated through disease-causing organisms and depends on salicylic acid (SA) and signal-transmitting compounds such as glycerol-3-phospate (G3P), while beneficial microbes induce ISR and are independent of SA [7]. The two forms of resistance are activated by different defense signals when the plant is attacked by pathogens [8], such as when it comes into contact with the glycerol-3-phosphate molecule.

The glycerol molecule that is produced and metabolized during the resistance induction step in plants is glycerol-3-phosphate (G3P). This molecule is produced during the process of phosphorylation of glycerol, which is mediated by the enzyme glycerol kinase (GK). GP3 can also be produced by the reduction of hydroxyacetone phosphate (DHAP), which is mediated by G3P dehydrogenase (G3Pdh) [9]. Glycerol has potential for disease control in the field, but the concentration must be carefully managed to avoid adverse or toxic effects. Nonetheless, given its natural property, it is highly environmentally friendly [10].

Currently, glycerol has been used in scientific research to promote tolerance/resistance to the main abiotic and biotic factors that affect plants. Its use has already been documented in systemic acquired resistance against *Phytophthora capsici* diseases in *Theobroma cacao* [11], coffee resistance to rust (*Hemileia vastatrix*) [12], and powdery mildew resistance in *Triticum aestivum* [10,13], among others.

Although the use of glycerol in plants is mainly related to disease control, the use of glycerol as a pesticide or a compound that can promote plant resistance/tolerance to the main biotic and abiotic factors is of paramount importance, given that it does not degrade in the environment and does not cause damage to human or animal health [10,11,13].

Therefore, systematically reviewing the theme "glycerol applied in agricultural and biological crops" is of great interest for understanding the mechanisms developed by plants to acquire resistance to biotic factors and the correlated pathways and protocols adopted in different studies. Thus, the main objective of this review was to gather articles published between 2008 and 2024 to compile the main data produced in agronomy and biology regarding the use of glycerol as a resistance-inducing molecule in plants.

2. Materials and Methods

The systematic review was conducted with the aid of StArt (*State of the Art through Systematic Review*) version Beta 3.0.3 software (http://lapes.dc.ufscar.br/tools/start_tool, accessed on 9 December 2023), developed at the Federal University of São Carlos (UFSCar). All procedures adopted by *start* followed the *Preferred Reporting Items for Systematic Reviews and Meta-Analyses* (PRISMA) guidelines, which allow reviews to be more transparent, with information on the reason for the review, the author's approach, and the information that the authors found (results). Thus, three steps were followed to prepare the review: planning, execution, and summarization.

2.1. Planning

At this stage, a protocol defined according to the following information was created: article title, authors, objective, keywords, research questions, research sources, inclusion/exclusion criteria, and definition of the type of study. The research question was What mechanisms are used by glycerol to create disease resistance in plants? Secondary questions were elaborated and are listed in Table 1.

Table 1. Issues raised about the activity of glycerol as an agent inducing plant disease resistance in a systematic review of studies published in the last 14 years.

Questions
1. Which countries have used glycerol for disease resistance induction?
2. What is the expected result or results using glycerol?
3. What techniques are being used for glycerol application?
4. What genes are reported in the plant's response to glycerol use?
5. Which pathogens have been controlled by glycerol?
6. Which crops use glycerol as a resistance inducer?
7. What protocols have been proposed for glycerol application?
8. What structural and biochemical mechanisms are associated with the use of glycerol?
9. What concentrations of glycerol are used to induce resistance in plants?

2.2. Implementation

This review considered studies conducted between 2008 and 2024 that conducted experimental research with the application of glycerol to evaluate the induction of resistance to plant diseases.

From the protocols established for the elaboration of the systematic review, two search *strings* were constructed based on the five inclusion components called "PICOS"—Population, Intervention, Comparison, Outcome, and Type of study [14] (Table 2).

Table 2. PICOS terms for the research question used in this systematic review on the activity of glycerol as a plant disease resistance-inducing agent published in the last 14 years.

Description	Abbreviation	Question Components
Population	P	Crops affected by diseases.
Interest/Intervention	I	The activity of glycerol as a plant disease resistance inducing agent for plant genetic improvement.
Comparison	C	Plant breeding methods that do not include the use of glycerol.
Outcome	O	Resistance to plant diseases.
Type of study	S	Scientific articles and literature reviews.

Database searches were conducted to select and extract articles. The databases used were CAPES journals (https://www.periodicos.capes.gov.br, accessed on 30 March 2024), PubMed Central (https://www.ncbi.nlm.nih.gov/pmc), Springer (https://link.springer.com, accessed on 30 October 2024), and Web of Science (https://www.webofscience.com/wos/woscc/basic-search, accessed on 30 October 2024). The Google Scholar website (https://scholar.google.com.br, accessed on 30 October 2024) was also used for our search. The websites were accessed in October 2024. The selected files were imported in BIBITEX and MEDILINE format compatible with *StArt* software-version Beta 3.0.3. In the search *strings*, connectors such as "AND" and "OR" were used to group synonymous keywords and main topics.

Two search *strings* were used: glycerol OR "G3P" OR "glycerol-3-phosphate" AND "plant resistance" AND "resistance induction" OR "systemic immunity in plants" OR "systemic acquired resistance" AND "plant disease" OR "plant pathogen" and glycerol OR G3P OR "glycerol-3-phosphate" OR "glycerol metabolism" OR "glycerol application" AND "disease resistance" OR "plant resistance" OR "plant diseases" or "biotics factors" OR "biotic stress" AND "systemic immunity in plants" OR "systemic acquired resistance"; the latter was used only for the Web of Science database. In both cases, the search *string* was designed to include a wide range of articles related to the use of glycerol as an agent inducing resistance to biotic stresses.

Subsequently, the selection and extraction steps were conducted, which were considered as inclusion criteria: (I) papers that contained the terms of the *string* in the title, abstract, and keywords; (I) articles that answered the questions of the protocol; (I) review articles. The exclusion criteria were (E) theses, dissertations, manuals; (E) book chapters; (E) duplicates; (E) avoiding the topic; (E) works without clear contribution; (E) works not written in English.

2.3. Summary

This step consisted of developing graphs, tables, and word clouds. The bar graphs were created in the R statistical program using the *ggplot2* (version 8.1) and ggpubr *packages* (version 0.6.0) [15]; due to the number of articles, the data are reported in numbers and not in percentages. The bibliometric map was generated in the VOSviewer_1.6.17 program [16]. The tables were created to display the results of the active mechanisms using glycerol, the forms of application of glycerol, and results obtained or expected with the use of glycerol. A word cloud with genes expressed in response to glycerol use was constructed with a free online generator, available at (https://www.wordclouds.com/).

3. Results

3.1. Database Search

The search carried out of the five databases generated a total of 2374 articles published between January 2008 and March 2022. On the Google Scholar website, 997 studies were found in the academic databases, 473 from Springer, 445 from PubMed central, 416 from CAPES journals, and 40 from the Web of Science. In addition, three studies that were not captured with the *string* were added manually (Figure 1).

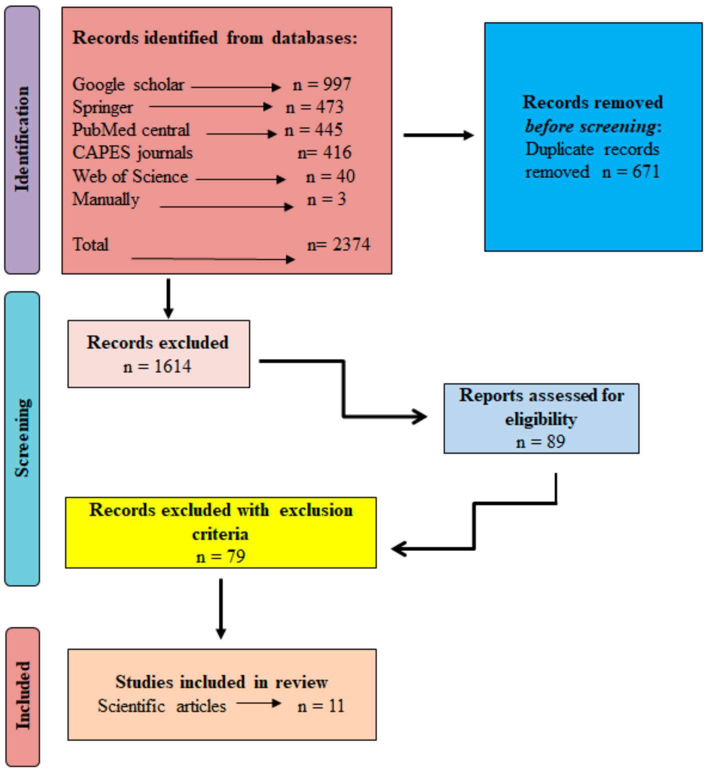

Figure 1. PRISMA flow diagram with the screening process of the articles selected for this systematic review on the use of glycerol as an inducer of disease resistance in plants.

In the first selection stage, 671 duplicate studies were excluded, and 1614 were excluded after reading the abstracts and keywords because they did not meet the inclusion criteria. In the extraction stage, 89 articles were analyzed, and, after reading the articles in total, 79 were excluded for not meeting the inclusion criteria. Thus, 10 articles were accepted for this systematic review (Figure 1), 3 of which were inserted manually. For consultation purposes, the manuscripts are stored in the link https://doi.org/10.5281/zenodo.10524571 (accessed on 26 June 2024).

A bibliometric map was created with keywords from the articles selected in the extraction step. This SR aimed to find studies of the application of glycerol to induce resistance to plant diseases. The highest frequency of studies generated was between 2008 and 2022 (Figure 2).

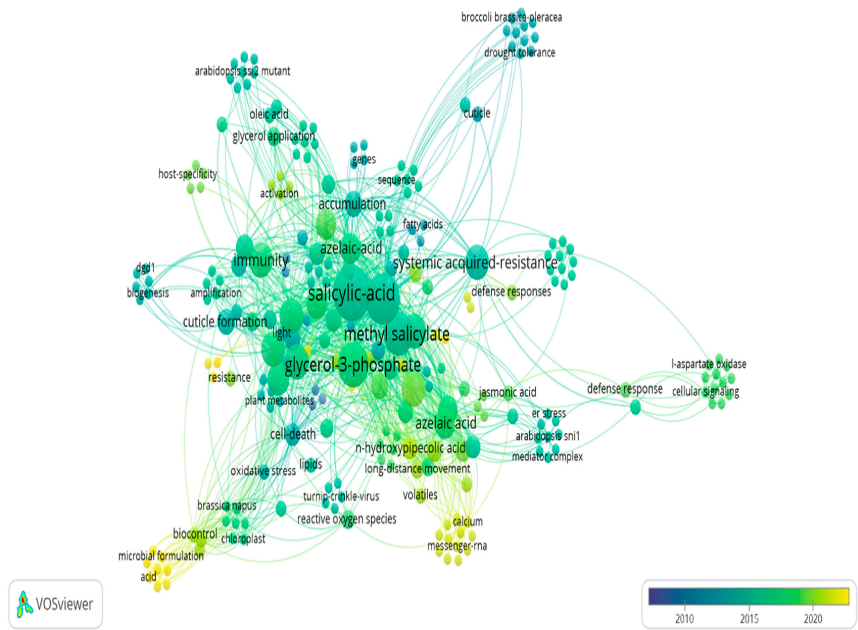

Figure 2. Bibliometric map of words from the selected articles on the use of glycerol as an inducer of resistance to plant diseases from 2008 to 2022.

The terms salicylic acid, methyl salicylate, and glycerol-3-phosphate were the most frequent and were related to azalaic acid, accumulation, genes, and systemic acquired resistance; in addition, they were related to the terms application of glycerol, oleic acid, and mutant Arabidopsis ssi2.

3.2. Study Sites

Most of the studies were conducted in the United States (5), followed by China and Japan, which had two articles each published on the use of glycerol as an inducer of disease resistance. In Brazil, only one study was found (Figure 3).

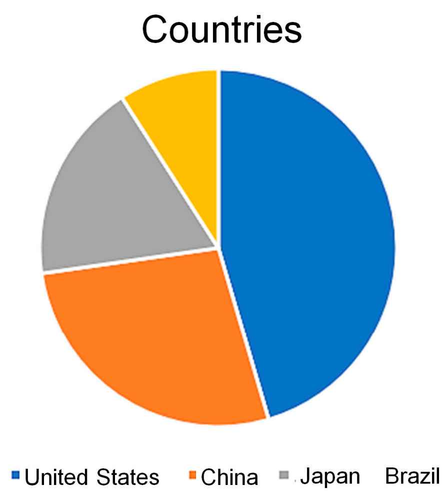

Figure 3. Countries that have conducted studies with glycerol as an inducer of plant disease resistance.

3.3. Crops Used

Among the most-used crops, the model plant, *Arabidopsis thaliana*, was the most studied (four articles), all conducted in the United States, followed by wheat and soybean (two). Coffee, rice, and cocoa were also studied regarding the use of glycerol as an inducer of resistance to plant diseases (Figure 4).

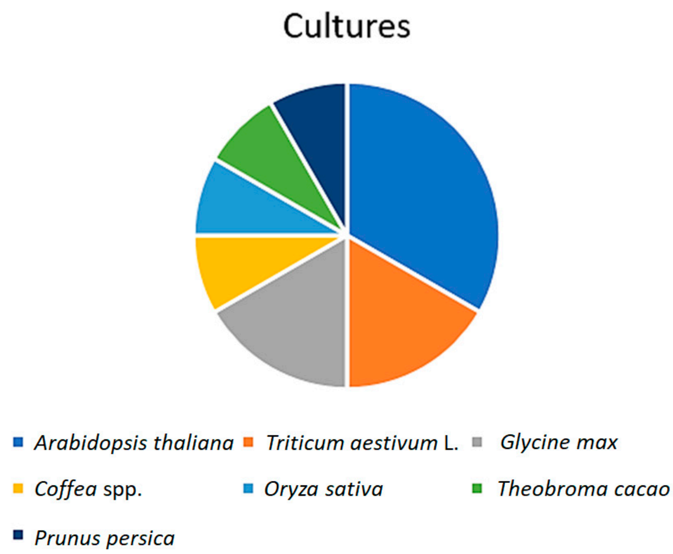

Figure 4. Cultures used in scientific studies on the application of glycerol to induce resistance to plant diseases.

3.4. Pathogens Studied

Among the most-studied pathogens, *Pseudomonas syringae* DC 3000, which causes bacterial spotting in *A. thaliana* and tomato, had the highest number of articles (four), followed by the pathogen *Blumeria graminis* f. sp. *tritici* (two), which causes powdery mildew. The pathogens *Phytophthora sojae*, *Phytophthora capsici*, *Hemileia vastatrix*, *Xanthomonas oryzae* pv. *Oryzae*, *Magnaporthe grisea*, *Brusone colletotrichum*, turnip crinkle virus, and Hyaloperonospora were also tested with glycerol (Figure 5).

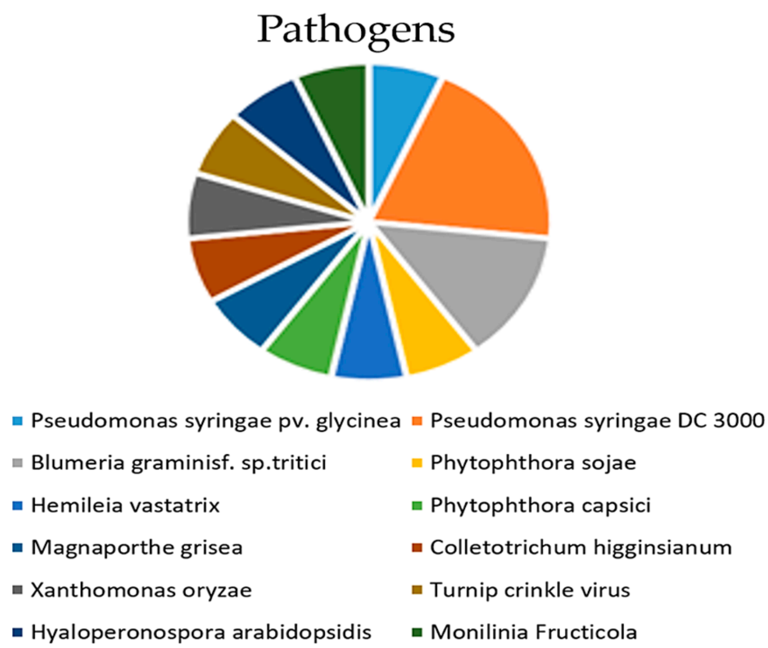

Figure 5. Most commonly used pathogens in studies evaluating plant resistance to diseases induced by glycerol.

3.5. Concentrations Used

Different concentrations of glycerol were used for resistance induction in the selected articles. Four used only a single concentration, 3%, 1%, or 0.46%; the last one was used in two studies. The other articles used two glycerol concentrations ranging from 0.004 to 9.21% (Figure 6).

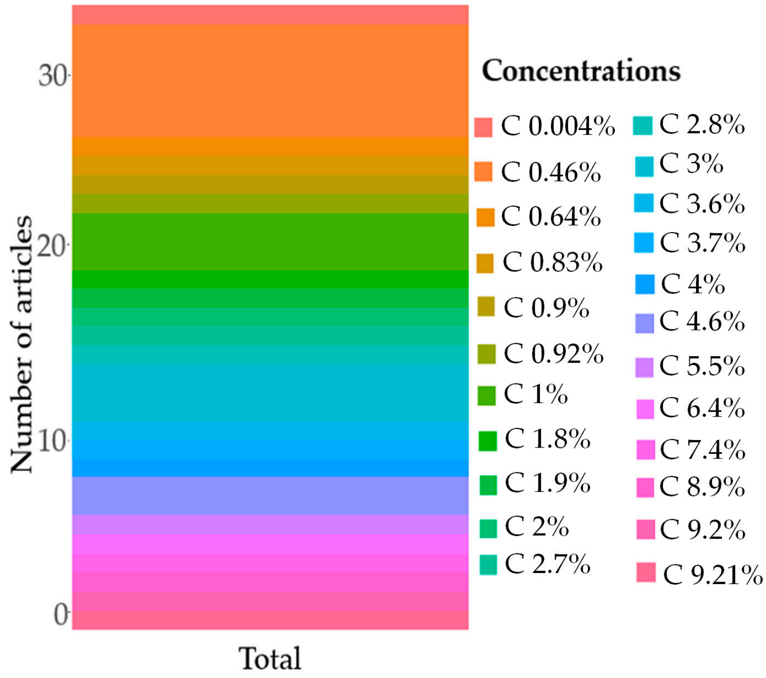

Figure 6. Frequency of glycerol concentrations used in studies on glycerol as a disease-resistance-inducing agent in plants.

3.6. Techniques Used

Among the techniques used to apply glycerol, spraying (using an uninformed container) was more frequent (eight studies) (Table 3). The other form of application used was immersion, in which leaves were immersed in 100 mL solution for 10 s every 24 h for three consecutive days.

Table 3. Techniques used for the application of glycerol in studies on the use of glycerol as an agent inducing resistance to plant diseases.

Technique Used	Study
Spraying	[13]
Not described	[12]
Immersion	[11]

3.7. Observed Results

Table 4 shows the results obtained with the use of glycerol to induce resistance, with the effects being similar, such as reduced disease lesions, programmed cell death, increased G3P levels, as well as decreased oleic acid (18:1) and gene expression levels.

Table 4. Results obtained in studies on the use of glycerol as an agent inducing resistance to plant diseases.

References	Observed Outcomes
[13]	Increased levels of JA and SA, reduced level of IAA and expressions of PR proteins.
[12]	Lower percentage of lesions.
[10]	Changes in the expression of genes associated with glycerol and fatty acid pathways; increase in G3P.
[11]	Increase in endogenous levels of G3P, ROS, and malondialdehyde (MDA) content and decrease in oleic acid levels.
[17]	Reduction in 18:1 levels and induction of nitric oxide accumulation in the chloroplasts of Col-0 plants.
[18]	Glycerol was unable to induce SAR in gli1 plants.
[19]	Increased resistance to *Magnaporthe grisea* and *Xanthomonas oryzae* pv. *oryzae* diseases.
[9]	Reduction of oleic acid (18:1) levels.
[20]	G3P increase. Higher resistance in both wild and gly1 types of *Arabidopsis thaliana* plants.
[21]	Appearance of visible and microscopic dead-cell-like lesions on treated leaves.

A word cloud with the genes related to plant resistance using glycerol was created, where the size of the name of each gene indicates the number of articles that describe the expression of the gene (Figure 7). The most commonly reported genes expressed in response to glycerol were *PR-1*, *CHI1*, *TAPR-1*, *PR-5*, *SCAM-5*, *Udp-glycosyltransferase*, *chitinase-1*, and *LOXA*.

Figure 7. Word cloud of resistance genes found in studies using glycerol as an inducer of plant disease resistance.

Among the structural and biochemical mechanisms reported by using glycerol were decreases in oleic acid levels and increases in glycerol-3-phosphate, which resulted in increased resistance with gene expression activity (Table 5).

Table 5. Structural and biochemical mechanisms associated with using glycerol as an agent inducing resistance to plant diseases.

References	Structural and Biochemical Mechanisms
[13]	Plant fatty acid metabolism, hormone crosstalk, and induction of pathogenesis-related genes.
[12]	Glycerol-3P-dependent resistance mechanism.
[10]	Signaling molecules: glycerol-3-phosphate (G3P) and oleic acid (18:1); reactive oxygen species (ROS).
[11]	Defense signaling pathway mediated by 18:1.
[17]	Increased endogenous G3P levels, 18:1 decrease, and ssi2-like phenotypes in control plants
[18]	Glycerol was unable to induce SAR in gli1 plants.
[19]	Reduction in oleic acid (18:1) levels.
[9]	Reduction in oleic acid (18:1) levels.
[21]	G3P increase.
[20]	Reduction in oleic acid (18:1) levels.

4. Discussion

4.1. Database Search

It is important to highlight that, so far, no literature reviews or systematic reviews have been found on glycerol as a molecule that induces disease resistance, a fact that reinforces the importance of this systematic review on the subject.

There have been many articles citing the word glycerol due to the presence of the molecule glycerol-3-phosphate (G3P), which also participates in the natural resistance induction pathway in plants. In addition to the molecule mentioned, many studies contained terms that contained words in the *string* such as systemic acquired resistance, plant diseases, and resistance induction in their title, abstract, or keywords. These are commonly used keywords when working with resistance in plants.

4.2. Study Sites, Cultures, and Hosts

Glycerol as a resistance inducer has been extensively studied in the United States (five studies); most have used the same phytopathogenic agent, *Pseudomonas syringae*, and the model plant, *Arabidopsis thaliana*. The *P. syringae* bacterium can infect different types of cultures, consisting of different pathovars, which explains the growing use of glycerol in an attempt to induce resistance in plants to this pathogen [22]. In addition, the use of glycerol in the pathositema *Theobroma cacao* × *Phytophthora capsici* was also studied. Cocoa is a commercially important crop due to its vast functionality and being the main raw material for chocolate [23].

China and Japan produced two works each. In China, the studies were conducted with the pathogen *Blumeria graminis* f. sp. *tritici* with an interval of four years between the studies with wheat as the crop. Wheat is one of the most important cereals in the world because it is one of the main sources of human food. In addition to powdery mildew, this crop is severely affected by *Puccinia striiformis*, striped rust, or yellow wheat rust [10].

The most studied crop using glycerol as an inducer of pathogen resistance in the last 14 years was the model plant *A. thaliana* (four articles). The articles using this plant focused on the fact that it has a short life cycle (six weeks). This facilitates its use in research in the area of genetics, biochemistry, and physiology, helping in the development of resistant, adapted, and productive cultivars through the transfer of the knowledge generated to other crops of food interest [24,25].

Essential food crops such as rice, wheat, and soybeans have also been studied for their resistance to pathogens in the presence of glycerol. Rice is grown under rainfed conditions in various agroclimatic zones and is subject to various biotic stresses that trigger morphophysiological and molecular responses that negatively affect growth and development and yield potential [26]. Therefore, global efforts to use conventional and/or biotechnological interventions to affect some of the characteristics of the pathogen stress responses have been made. Soybeans also have great economic value, not only in human food but also animal feed, and can produce products such as oil, milk, vegetable protein, and biofuels [27].

The studies carried out in Japan were on soybean and rice crops, the main foods that are part of the diets of humans and animals [28,29]. In the rice crop, the pathogens *Magnaporthe grisea* (race 007.0) and *Xanthomonas oryzae* (strain T7174) were studied, and, in the soybean crop, *Pseudomonas syringae* DC 3000.

Coffee, a crop studied in Brazil regarding the use of glycerol, is one of the first plants grown in Brazilian regions. The crop gained prominence worldwide, being cultivated for export by several countries, becoming essential for farming families [30].

4.3. Glycerol Doses and Concentrations

Different concentrations of glycerol were used for resistance induction in the selected articles. Four used only a single concentration, 3%, 1%, or 0.46%; the last of these was used in two studies. The most efficient glycerol doses in resistance induction studies were reported by Zhang et al. [11], Li et al. [10], and Gazolla et al. [12] in the cocoa, wheat, and coffee crops, respectively. The doses of 0.92 and 3% induced resistance in plants, making it clear that each crop infected by different pathogens responds differently to the concentrations used. When comparing the results of these studies, the 3% dose can be considered the most efficient for use, including in future studies, due to its high rate of resistance induction and low toxicity in the plants studied to date [10,12,13].

In addition to glycerol, the fixative product Silwett L-77 was used. This product is used as a patch so that the product of interest can better adhere to the plant, contributing to better absorption. The concentrations that were used of this product were 0.02 and 0.04%. Venugopal et al. [9], Chanda et al. [18], Chanda et al. [21], and Mandal et al. [31] did not use any fixative product in their studies (Table 3).

Since, in most studies, glycerol was applied with the addition of Silwett L-77, its efficiency was not related to the use of the product, and it cannot be stated that without Silwett L-77, the induction of resistance would be lower. The glycerol concentrations in most studies were not defined in percentages: they were given in millimolar (mM) and micromolar (µM). However, this systematic review transformed them into percentages for uniformity and standardization.

Of the numerous concentrations used, the concentrations of 2–4% were the ones that stood out the most. Gazolla et al. [12] used 1 and 3%, and they obtained better results at the concentration of 3%, making susceptible coffee plants resistant to rust (*Hemileia vastatrix*).

Using doses of glycerol of 1–4% in wheat plants in the seedling and adult phase, the higher the dose, the greater the degree of resistance, but with a higher dose, there was yellowing of the leaf tips, which led to consider the 3% treatment as the best dose. Thus, in the subsequent experiments, only the 3% dose was used before and after inoculation. The time of application that resulted in the greatest resistance was 1–2 days prior to inoculation. The application on the same day of inoculation and after did not produce positive results regarding compared with those applied before the existence of the fungus. However, for better resistance in plants under continuous infection, it was necessary to apply a 3% dose 1 day before inoculation and 3 days after the first application [10].

The effect of glycerol was positive not only in seedlings and in adulthood but also in other wheat varieties (Chinese spring, Jimai5265, Liaochun 10, and durum wheat Mo75). Concentrations of 2.5–3% resulted in resistance in the seedling phase but affected root and shoot development [10].

Glycerol is considered toxic depending on the concentration used and the stage of plant development [32]. Phytotoxicity occurred in wild *Arabidopsis thaliana* plants, where glycerol inhibited root development, decreasing the production level of auxin, a phytohormone responsible for plant elongation, in addition to altering the cell division of the root meristem [33].

Li et al. [13] used a dose of 3% glycerol in wheat. The results were positive, and the difference between the control and glycerol treatment was significant, where the germination rate of powdery mildew spores (*Blumeria graminis* f. sp. *Tritici* (Bgt)) in water-treated wheat leaves was approximately 90%, but 10.7% when treated with glycerol.

Zhang et al. [11] used the concentrations of 100 µM, 500 µM, 1000 µM, 50 mM, 70 mM, and 90 mM, which are equivalent to 0.46, 0.64, 0.83, 0.92, 4.6, and 9.2%, respectively, in cocoa plants to evaluate resistance to the fungus *Phytophthora capsica*, where they obtained the best results with the dose of 0.92%.

The concentration of 1% was sufficient for *gene* expression and resistance induction for the two diseases studied, blast and leaf rust, in wild rice culture [19]. Chanda et al. [21] used a 0.92% dose and were able to obtain positive results in wild-type and gli1 plants, where resistance increased with the application of glycerol.

The use of glycerol at 1 and 3% concentrations in a coffee crop resulted in resistance induction in the plants treated at a concentration of 3%. The resistance was explained by the increase in glycerol-3-phosphate, similar to that in the resistant cultivar [12]. G3P has already been confirmed as a signaling molecule contributing to systemic acquired resistance (SAR) in wheat plants against *Puccinia striiformis* f. sp. *tritici* [10,13].

Chanda et al. [21] used only a dose of 50 mM glycerol prepared with sterile water. The authors did not make clear their reason for choosing the dose but mentioned that using glycerol in large quantities on a plant can be used beneficially by the pathogen, for example, as a carbon source, promoting increases in the symptoms of the disease. Venugopal et al. [9], who were also part of the previously mentioned work, used the same dose. Years later, Chanda et al. [18] tested different concentrations of glycerol (500 µM, 50 µM, and 50 mM) but related the new results to the new doses tested compared with previous research.

4.4. Results Reported in the Studies

The exogenous application of glycerol in inducing resistance to pathogens by plants has been studied. Resistance occurred through gene induction, reduced oleic acid (18:1) levels, and increased G3P molecules in plants. When subjected to biotic stress, plants may have responses that allow the remodulation of fluid membranes. This modification of membrane fluidity is mediated by changes in unsaturated fatty acid levels, which rely on the action of fatty acid desaturation enzymes. The fine tuning of membrane fluidity maintains an environment conducive to the integral functions of proteins during stress. Therefore, the modulation of chloroplast oleic acid (18:1) levels is paramount for normal protein expression in the responses to pathogens [34].

In addition, fatty acids, working as a source of energy, are fundamental components of cell membranes, suberins, and cutin sera, considered barriers between the plant and the environment. Recent studies have demonstrated that free (18:1) oleic acid levels in the chloroplasts regulate the defense responses of plants to pathogens, including programmed cell death and SAR [35,36]. Reduced levels of 18:1 oleic acid have been found to be responsible for the constitutive activation of plant defense responses [9,37].

In two studies by Chanda et al. [18,21], they verified that there was no induction of resistance in Arabidopsis mutant plants (gli1), as they could not convert glycerol to G3P, perhaps due to the low production of the enzymes glycerol kinase (GK) and G3P dehydrogenase, G3Pdh, which convert glycerol into G3P [31]. Glycerol induced the production of salicylic acid (SA) and jasmonic acid (JA) in wheat plants, in addition to reducing auxin (indol acetic acid (IAA)). In this work, they also identified the induction of proteins related to pathogenicity [13].

The hormones SA, JA, and ethylene (ET) are responsible for the signals that trigger plant defense responses. SA expresses proteins (PR), while JA and ET are signaling pathways activated by injuries [38]. The decrease in the level of IAA did not have a negative effect on the plant. Its decrease may have been caused by SA, which, in the presence of the two hormones in the plant, limits the production of one of them [39].

Li et al. [10] applied glycerol before and after inoculation in wheat against *Blumeria graminis* f. sp. *Tritici* and obtained positive results with a concentration of 3%. Resistance was induced by glycerol-3-phosphate molecules at high and low levels of 18:1 oleic acid.

Application preceded infection by performed 1 to 2 days and then was performed once every 4 days. There was induction of reactive oxygen species (ROS) and salicylic acid accumulation, which is an important molecule for inducing systemic acquired resistance.

In studies of wheat resistance to powdery mildew, Li et al. [13] evaluated the leaf transcriptome in glycerol-activated immunity. It was possible to identify transcripts such as TaGLI1, TaACT1, and TaSSI2, which participate in the metabolism of glycerol and fatty acids (FAs), which may contribute to the accumulation of G3P and 18:1. According to a Gene Ontology study, glycerol induced a response to jasmonic acid (JA), a defense response to bacteria, lipid oxidation, and a factor that is not related to resistance or growth. It induced the accumulation of JA and the salicylic acid (SA) level and reduced the amount of auxin hormone (IAA) in wheat plants.

The results of Zhang et al. [11] in *T. cacau* × *Phytophthora capsici* were positive, depending on the dosage, where there was the expression of resistance genes and activation of the reactive oxygen species (ROS) pathway. Depending on the dosage used, the increase in the level of G3P and the decrease in oleic acid (18:1) ere noticeable. Using the dosages of 100, 500, and 1000 mM, there was no difference in the size of the lesions, and it can be concluded that the increase in concentration did not make a difference and that the concentration of 100 mM is sufficient to trigger resistance pathways.

Studying the systemic factors induced by glycerol in cocoa against *Phytophthora capsici*, Zhang et al. [11] found that the product was not able to activate the resistance pathways in the distal tissues that were untreated, signaling that all leaves should be treated with glycerol. The distal leaves did not differ in the levels of G3P, oleic acid, or ROS compared to the control. In this case, G3P did not act as a mobile inducer of resistance in a cocoa crop. Chanda et al. [18] confirmed that G3P is able to move to other tissues, activating the pathway of systemic acquired resistance against secondary infection.

As in other studies, the reduction in oleic acid due to the application of glycerol was noted in the work by Kachroo et al. [20]; it was no different in soybean plants, demonstrating once again that the higher the glycerol dose, the lower the oleic acid (18:1) level. Due to glycerol treatment, plants showed dead cell-like lesions. According to the authors, this was related to increased ROS and the induction of *PR-1*, *PR-1a*, *SCaM-4*, and *SCaM-5* genes. Glycerol caused the plants to become resistant to bacterial pathogens and oomycetes. There was a reduction in susceptibility and a survival of more than 80% in the treated plants. The concentration of 100 mM was considered better, being used in later studies [20].

Jiang et al. [19], evaluating the responses of glycerol-treated rice plants to disease resistance, blast, and leaf burning, had positive results with increased expression of resistance genes and reduction sin oleic acid levels (18:1). Gazolla et al. [12], testing two concentrations of glycerol in susceptible coffee plants, reported that the application of glycerol induced resistance similar to that the resistant cultivar, identifying the importance of G3P in disease resistance and the efficiency of application before inoculation.

Negative results were found in *Arabidopsis* mutant gli1 plants as they were unable to convert glycerol to G3P [21] in the defense against the hemibiotrophic fungus *Colletotrichum higginsianum*. The same occurred in the study by Chanda et al. [18] when they tested SAR in *Arabidopsis* mutant plants against the bacterium *Pseudomonas syringae* DC 3000, where gli plants were susceptible because they were not able to metabolize glycerol into G3P, which prevented glycerol from being effective in SAR. Xia et al. [40] found that *Arabidopsis* mutant plants were defective in the production of acyl protein (ACP4), a critical component of fatty acid (FA) biosynthesis, impairing cuticle formation in leaves. Thus, the plants produced the resistance signal but could not receive it, being impaired at the beginning of SAR.

The application of glycerol decreased oleic acid (18:1) levels and induced the accumulation of nitric oxide (NO) in *Arabidopsis* plants against the bacterium *Pseudomonas syringae* DC 3000 [31]. Nitric oxide (NO) is a molecule that participates in several processes, such as germination, flowering, as well as opening and closing of stomata, including the defense of plants against pathogens [41].

Mandal et al. [31], in their study with *Arabidopsis*, demonstrated the relationship between 18:1 oleic acid and NO-mediated defense signaling pathways, where oleic acid (18:1) synthesized in the chloroplast regulated the stability of the protein associated with nitric oxide (NOA1) and consequently the biosynthesis and accumulation of NO, leading to more resistance of the plant to diseases. In addition, when comparing these results of the exogenous application of glycerol with those of other products such as mannitol and sorbitol, which do not reduce the amount of 18:1 oleic acid, there was no accumulation of the NO signaling molecule.

4.5. Genes Expressed in Response to Resistance Induced by the Use of Glycerol

The most commonly reported expressed genes in response to glycerol were *PR-1*, *CHI1*, *TAPR-1*, *PR-5*, *SCAM-5*, *Udp-glycosyltransferase*, *chitinase-1*, *and LOX*. From the works that performed gene expression analysis, several genes were identified in response to infection when treated with glycerol. The *PR-1* gene was the most expressed, which is a gene already known for being highly induced in infected plants when in its basic form [42]. PR-1, one of the members of the 17 pathogen-related (PR) protein families, is present in all plants at the time of defense against pathogen attacks [42].

Calmodulin (*CaM*) is a Ca^{2+}-dependent protein, and its isoforms, *SCaM-4* and *SCaM-5*, are activated by pathogen elicitors during infection. Constitutive expression in tobacco demonstrated its participation in the induction of lesions and the expression of genes associated with SAR [43]. In the study by Kachroo et al. [20], soybean plants treated with glycerol showed cell death lesions, which correlated with the expression of the *PR-1* and *PR-1a* genes. With treatment with 50, 100, 200, 300, and 400 mM glycerol every 24 h for 3 days, the *SCaM-4* and *SCaM-5* genes were also expressed [20].

Of the genes expressed in response to salicylic acid, there were none that were expressed in response to jasmonic acid. One study evaluated *PR-1* during *Phytophthora capsici* infection in Panniyur-1 plants and found that this gene was activated at the initial time of infection, such as PTI [42].

Other genes induced after glycerol treatment were identified in wheat plants. *Hsp70*, *pox*, and *LOX6* were induced even before systemic acquired resistance was activated [13]. The *LOX6* gene is involved in defending the plant against insect attacks, signaling wounds from long distances, in addition to being important in the initial accumulation of jasmonate (JA) and jasmonoyl-isoleucine (JA-Ile) [44,45].

The *HSP70* and *HSP90* genes are activated when the plant undergoes heat shock (HSIR). Widiastuti et al. [46] found that when plants were subjected to heat shock, this gene was induced after 12 h of treatment. After glycerol treatment, the *LOX* gene expressed in wheat plants was found to be an important component in the JA pathway for phytohormone production [47].

Li et al. [10], evaluating wheat plants treated with 1, 2, 3, and 4% glycerol in the defense response against powdery mildew, evaluated resistance through the *TaGLI1* gene before and after inoculation, and gene expression analysis revealed that 24 h after inoculation, the expression of this gene was higher than at 0 h [10], demonstrating a plant defense response in the presence of the pathogen.

The differences in gene expression when comparing glycerol-treated leaves and water-treated leaves were quite noticeable. The expression of R genes in wheat plants was 3.6% higher in glycerol-treated leaves. The *TaPR-2A* gene was expressed almost 10× more than in the water-treated control, demonstrating the efficiency of glycerol in the control of powdery mildew [10]. *Blumeria graminis*, which causes powdery mildew, is a biotrophic pathogen that locally and systemically activates the pathway of genes such as *PR2*, contributing to systemic acquired resistance [48].

Li et al. [13], evaluating the induction of wheat resistance to powdery mildew by the treatment of only 3% glycerol, found that the genes expressed after infection are important for resistance, as they contribute to the production of resistance-inducing molecules such as G3P and fatty acids, and to the systemic acquired resistance by activating pathways associated with ROS accumulation and cell death. The *WRKY45* and *PR1b* genes were expressed in rice plants as a resistance response to bacterial blasts and wilt diseases [19].

Pathogenesis-related genes (*PR* genes) were expressed together after applying glycerol to cocoa plants for resistance to *Phytophthora capsici*, where Zhang et al. [11] identified up to a 4174-fold increase in plants treated with the 500 mM dose. Gene expression was dose-dependent. At the lowest dose of 100 mM, the *PR*-3Q and *PR*-5 genes were not significantly induced in cocoa. The expression of *TcCHi4* was significant at the two doses of 100 and 500 mM, being five and thirty times higher. Chitinase genes were also expressed in wheat against the pathogenic fungus *Phytophthora capsica* [13]. *CHI* genes are pathogenesis-related proteins whose function is to degrade the chitin compound, which is present in the cell wall of some bacteria and most fungi [47,49].

4.6. Techniques Used for Glycerol Application

Of the 11 studies found on the use of glycerol in plants for resistance induction, only 1 did not specify the technique used; the others used the spraying and immersion techniques. The object used for spraying the product was not specified. Although immersion was rarely used for the application of glycerol, it is a technique considered more effective because it remains in contact longer with the area of interest; for a spray to have similar results, several applications are necessary for the production of layers [50].

Li et al. [10] prepared glycerol solution (with sterile water and 0.02% Silwett L-77) for use in wheat plants for mildew resistance (Bgt). The control treatment was water containing only Silwett L-77. Treatments were applied until runoff from the leaves. Inoculation occurred one day after pretreatment and after inoculation, with four applications.

Li et al. [13] sprayed a solution with 3% glycerol containing 0.02% Silwett L-77 on wheat plants for resistance to powdery mildew (Bgt). For the control treatment, the water also contained Silwett L-77. Seedlings with fully expanded leaves received the treatments twice (once daily) until liquid ran off from the leaves.

Developing cocoa plants were treated with glycerol dissolved in sterile water containing 0.04% Silwett L-77. The water treatment also contained 0.04% Silwett L-77. The immersion technique was used with 100 mL solutions, immersing leaves for 10 s every 24 h for 3 days [11].

Also using 0.04% Silwett L-77 in soybean plants at the V1 growth stage, Kachroo et al. [20] applied glycerol with sprays every 24 h for 3 days to achieve resistance to the pathogens *Pseudomonas syringae* pv. *glycinea* and *Phytophthora sojae*. Based on the work of Jiang et al. [19], Kachroo et al. [20] made some modifications to the methodology using only a 1% concentration. The concentration of Silwett L-77 was 2%, and application was performed once daily for two consecutive days on rice plants with four or six leaves.

Chanda et al. [21] and Venugopal et al. [9] sprayed 50 mM glycerol and sterile water on *Arabidopsis* plants for inoculation against *C. higginsianum*. Mendel et al. [17] used 100 µM, 500 µM, 1000 µM and 50 mM glycerol in wild-type plants and *Arabidopsis* mutants for resistance to *Pseudomonas syringae* DC 3000. Chanda et al. [18] also used the glycerol spraying technique at 500 µM, 50 mM, or 50 µM in soybean plants for resistance induction against *Pseudomonas syringae* DC 3000. Gazolla et al. [12] did not describe the methodology used but reported that they applied 1 and 3% glycerol dosages for resistance to coffee rust.

4.7. Biochemical Mechanisms Participating in the Resistance Pathway in Glycerol-Treated Plants

In some studies, the biochemical effects of glycerol for disease resistance were related to the reduction in oleic acid (18:1) in the induction of resistance. In addition to oleic acid (18:1), other metabolites of fatty acids (FAs), plant hormones, and genes related to pathogenesis were present. Oleic acid (18:1) is an unsaturated fatty acid (UFA) and has both positive and negative effects on plants. It performs functions in the plant against biotic and abiotic stresses. It can also increase oxidative stress, which compromises plant cells, hinders the photosynthetic process, and even induces genetic mutation [51].

Glycerol application, resulting from the increase in G3P, always decreases the production of oleic acid (18:1), and this decrease is beneficial in the plant's defense process against pathogens. Its decrease occurs with the encoded stearoyl-acyl transporter desaturase protein (SACPD) mutation, which induces constitutive defense by activating gene expression [21]. In *Arabidopsis* mutant plants, decreased oleic acid caused elevated expression of the SA-mediated *PR1* gene,; this biochemical process takes place in the plastids, involving the acylation of G3P, with oleic acid and signaling mediated by salicylic acid, also involving jasmonic acid [52].

The acylation between oleic acid and glycerol-3-phosphate is important in the defense process of plants. When acylation does not occur, such as in *act1* plants, the expression of defense genes, such as *PR1*, does not increase due to the lack of SA induction [21].

Oleic acid, along with other fatty acids (linolenic acid and linoleic acid) have been applied to plants to decrease the growth of phytopathogenic fungi. Fatty acids have been shown to inhibit the development of microorganisms, but the mechanism that causes this phenomenon has not been discovered to date [53]. Inhibition does not happen with all fatty acids. In some cases, as in the work of [54], the authors found that when oleic acid was used, there was no significant decrease in the development of the pathogen, as occurred with other acids.

In the studies evaluated, glycerol activity was related to the activation of disease resistance induction pathways, with genes and proteins related to pathogenicity. In addition, resistance was related to an increase in G3P and a decrease in oleic acid (18:1) levels [11,19].

G3P participates as a signal in systemic acquired resistance to prevent secondary infections. In resistance against undesirable rhizobia, G3P relies on a previously unknown signal to induce its accumulation and activate SAR in the aerial part of the plant, then returns to the roots and eliminates nonbeneficial rhizobia [55].

The exogenous use of glycerol has been related to the decrease in oleic acid (18:1). Its low level increases resistance through the expression of *R* genes without requiring the presence of SA [21]. Li et al. [10] found this with the decrease in oleic acid (18:1) in plants infected with powdery mildew treated with glycerol compared to plants treated with water.

The results show that glycerol has significant potential to be applied as a substitute or additive in agricultural products, increasing the levels of oleic acid (18:1), thus inducing resistance in plants.

More research is needed to bring this technology to commercialization including on dosage, timing, and application intervals, which need to be characterized, Recent studies have confirmed that the use of glycerol in plants is effective in inducing resistance against diseases. For example, it has been discovered that glycerol has the potential to stimulate resistance in peach plants against the fungus *Monilinia fructicola* [56]. In addition, other genes related to plant resistance should be studied, and the action of oleic acid in plant defenses against pathogens should be characterized in detail.

5. Final Considerations and Future Perspectives

Biotic stresses cause large crop production losses, which require new strategies to support plant tolerance/resistance. The use of glycerol as a resistance-inducing molecule can help plant breeding, as the product is applied exogenously, whether in the seedling or adult phase. Glycerol has positive effects when used at the right time and in the correct dosage.

This SR included 10 studies found in databases published in the last 14 years. Among the most-studied crops for glycerol application, *Arabidopsis thaliana*, *Glycine max*, and *Coffea* spp. stand out, calling attention to the fact that despite the positive results, there have been few studies using glycerol as an inducer of resistance in plants against biotic factors in agricultural species.

Among the most-studied biotic agents, *Pseudomonas syringae*, consisting of different pathovars that can infect different types of crops, stands out. This explains the growing use of glycerol in an attempt to induce resistance in plants against this pathogen in addition to pathogens such as *Blumeria graminis* and *Colletotrichum higginsianum*, which have been also reported.

Glycerol concentrations ranged from 0.004 to 9.21%, with the concentration of 3% being considered effective for most plant species. An increase in G3P and a decrease in oleic acid levels have generally been seen in plants with increased resistance to pathogens. Among the main means of application of the product, spraying and immersion stood out. These will be easy to apply in future works.

The use of glycerol can alter plant hormone signaling pathways, increasing jasmonic and salicylic acid and reducing IAA levels. Although some studies did not evaluate gene expression, it was possible through those who did to identify genes that played roles in the resistance process from the use of glycerol. Among them, the most reported were *PRs* (*PR-1*, *PR2*, *PR-5*, etc.), *HPS70*, *HSP90*, *SCAM4* and *Tapr1*. These glycerol-induced changes probably contributed to resistance in several plant species.

The various crops reported in this SR are susceptible to many diseases, which cause significant yield losses, with the exception of the model plant *A. thaliana*. A low-cost and effective strategy for biotic stress management is therefore very much needed. Notably, in this aspect, glycerol is suitable for use as a cosolvent material in the application of agrochemicals. Above all, glycerol seems to have some potential to be applied in the field as an environmentally friendly agricultural chemical to help control plant diseases. The results observed here provide evidence that suggests that glycerol has great potential to be applied as a substitute or additive in current agricultural chemicals.

Furthermore, we would like to emphasize that fungal plant pathogens are among the major factors limiting the productivity of agro-ecosystems, being responsible for widespread diseases. The renewed interest in glycerol as a substrate or medium complement is fueled by the low price of glycerol in agriculture and the growing search for environmentally friendly approaches.

We believe, and as more and more works are being published on the topic, that it is just a matter of time before the agricultural community starts to reap the benefits of the use of glycerol, and this SR will contribute to instigating greater interest in the topic. Times are changing, and the need for more natural approaches in agriculture is of utmost importance. There is no doubt that the benefits of the use of glycerol outweighs its drawbacks, and researchers and crop growers worldwide will greatly benefit from a low-cost, environmentally friendly approach to plant defense.

Author Contributions: Writing, preparation, and original draft: A.P.d.S.N., F.d.S.N., A.d.J.R., A.P.d.S.R., E.P.A. and C.F.F.; methodology, A.P.d.S.N., F.d.S.N., A.d.J.R., A.P.d.S.R., A.d.S.R., L.d.S.R., J.M.d.S.S. and L.C.d.S.J.; data analysis: A.P.d.S.N., F.d.S.N., A.d.J.R. and A.P.d.S.R.; and conceptualization: T.A.d.O.M. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by IITA/The Bill and Melinda Gates Foundation-Accelerated Breeding of Better Bananas. ID OPP1093845.

Data Availability Statement: Data will be made available upon request. The processed data are publicly available at https://doi.org/10.5281/zenodo.10524571.

Acknowledgments: We thank the Federal University of Recôncavo da Bahia and the Graduate Program in Plant Genetic Resources. Embrapa Mandioca e Fruticultura for the technical and laboratory support of this research; we thank the Improvement of Higher Education Personnel and research (CAPES and CNPq) and the Bahia State Research Support Foundation for granting the scholarships (FAPESB).

Conflicts of Interest: The authors declare no conflicts of interest.

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