



Review

Unlocking plant defenses: Harnessing the power of beneficial microorganisms for induced systemic resistance in vegetables – A systematic review

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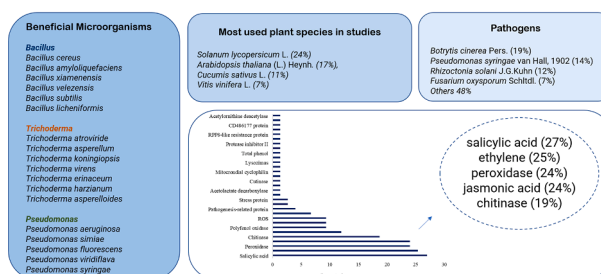
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HIGHLIGHTS

- Species in *Trichoderma*, *Bacillus*, and *Pseudomonas* induce systemic resistance in plants.
- *Solanum lycopersicum* was the most extensively studied species in induced systemic resistance.
- A total of 143 plant genes correlated with induced systemic resistance were identified.
- Hormones, enzymes, proteins, and reactive oxygen species are associated with ISR.

GRAPHICAL ABSTRACT

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ABSTRACT

Plants are susceptible to pathogen attacks, which employ strategies that overcome plant defenses and result in damage and losses. The use of beneficial microorganisms can induce systemic plant resistance, leading to greater efficiency in disease control. The objective of this study was to identify the main microorganisms that induce systemic resistance and the genes and metabolites involved in this process. A bibliographic search was conducted on the Scopus and Web of Science platforms, and the metadata were evaluated using the Bibliometrix package in R software. Subsequently, an investigation was carried out on the microorganisms and their interactions with gene expression and metabolites involved in plant defense systems. In studies of induced systemic resistance, the most cited beneficial microorganisms were *Trichoderma*, *Bacillus*, and *Pseudomonas*, and the most used plant were *Solanum lycopersicum* L. followed by *Arabidopsis thaliana*. Among the pathogens, the most employed were *Botrytis cinerea*, *Pseudomonas syringae*, *Rhizoctonia solani*, and *Fusarium oxysporum*. Beneficial microorganisms influence the expression of genes responsible for signaling jasmonic acid, salicylic acid, ethylene, and the production of enzymes involved in the complex of reactive oxygen species as mediators of protection.

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1. Introduction

Plants have developed a defense system to withstand both biotic and abiotic stresses. This system is activated through the signaling of hormones and metabolites, initiating a series of reactions that enable plants to shield themselves from these adversities (Pandey et al., 2017; Tiwari et al., 2022). As an example, we can cite the process that takes place during pathogen infection. Enzymes responsible for degrading cell walls are activated, leading to the formation of a barrier that impedes the further spread of the infection (Anjali et al., 2023). Just as genes start to be expressed, they collectively encode and facilitate plant resistance against harmful organisms (Li et al., 2022; Yu et al., 2022).

However, pathogens also activate virulence genes, which are responsible for producing effector proteins capable of suppressing plant immunity (Hale et al., 2023; Nirwan et al., 2023; Wu et al., 2021; Person et al., 1962). Just as pathogens can also generate interference RNAs that modify gene expression in plants, affecting the signaling and synthesis of metabolites tasked with inhibiting their attack (Wang et al., 2018; Weiberg et al., 2013). The rapid evolution of these effector genes, in comparison to host resistance genes, gives them a selective advantage (Schulze-Lefert and Panstruga, 2011; Zhang et al., 2023).

Furthermore, plants have also established symbiotic relationships with beneficial microorganisms, which can interact by promoting their growth, providing nutrients, and assisting in pest and disease control (Abedini et al., 2021; Mourouzidou et al., 2023). Disease control can be achieved through the direct management of the phytopathogen, which involves reducing its population through competition and the production of lethal or inhibitory substances (Jack and Nelson, 2018; Sharma et al., 2018; Wei et al., 2023), or through induced systemic resistance (ISR) (Akram et al., 2023; Morales-Cedeño et al., 2021; Poulaki and Tjamos, 2023).

ISR was initially distinguished from systemically acquired resistance (SAR), which is the resistance triggered by pathogens (Knoester et al., 1999). Both inducers elicit responses from the plant's defense system, leading to heightened resistance against pathogens through the signaling of growth regulators. However, SAR initiates a localized reaction characterized by the buildup of salicylic acid and the production of pathogenicity-related gene products, resulting in a hypersensitive response. This manifests in visible symptoms at the infection site. On the other hand, ISR involves signaling through jasmonic acid/ethylene or

ethylene/salicylic acid, or both combinations, which activate pathogenicity-related genes responsible for producing proteins that mitigate damage caused by free radicals. As a result, ISR protects plant cell walls without producing visible symptoms (Elhamouly et al., 2022; Hemmati et al., 2023; Salwan et al., 2023; Salwan et al., 2022). Despite the knowledge we have about ISR, there is still much to be clarified.

Comprehending which microorganisms induce ISR and how they influence plant defense system responses facilitates the development of effective biotechnological products for disease control. Such products can be employed in biological control, aligning with the United Nations' Sustainable Development Goals (SDGs) objectives 2, 3, and 15 (United Nations. "Transforming Our World: The 2030 Agenda for Sustainable Development." 2015. sustainabledevelopment.un.org. <https://sustainabledevelopment.un.org/post2015/transformingourworld>).

In this context, this systematic review aims to pinpoint the principal microorganisms that induce resistance, as well as the genes and metabolites implicated in this process.

2. Methods

2.1. Literature review

The literature review was conducted in March 2023 using the indexing platforms Scopus (<https://www.scopus.com>) and Web of Science (<https://www.webofknowledge.com>), using the Boolean search query ((induced systemic resistance) AND (secondary metabolites) AND (beneficial microorganism OR antagonist) AND (resistance genes)). The search encompassed the title, abstract, and keywords. Articles published in Portuguese, English, and Spanish were considered, and no specific time frame was imposed (Fig. 1).

The metadata was exported in BibTeX format and then analyzed using the R software with the Bibliometrix package (Aria and Cuccurullo, 2017). Duplicate files were removed, and a single file was generated. Following this, the eligibility of the articles was assessed based on the following inclusion criteria: (a) The articles must pertain to induced systemic resistance; (b) ISR must be induced by a beneficial microorganism; (c) The work must address genes or secondary metabolites involved in plant defense systems.

Subsequently, an evaluation of the annual scientific production was conducted, and the impact of publications along with the number of

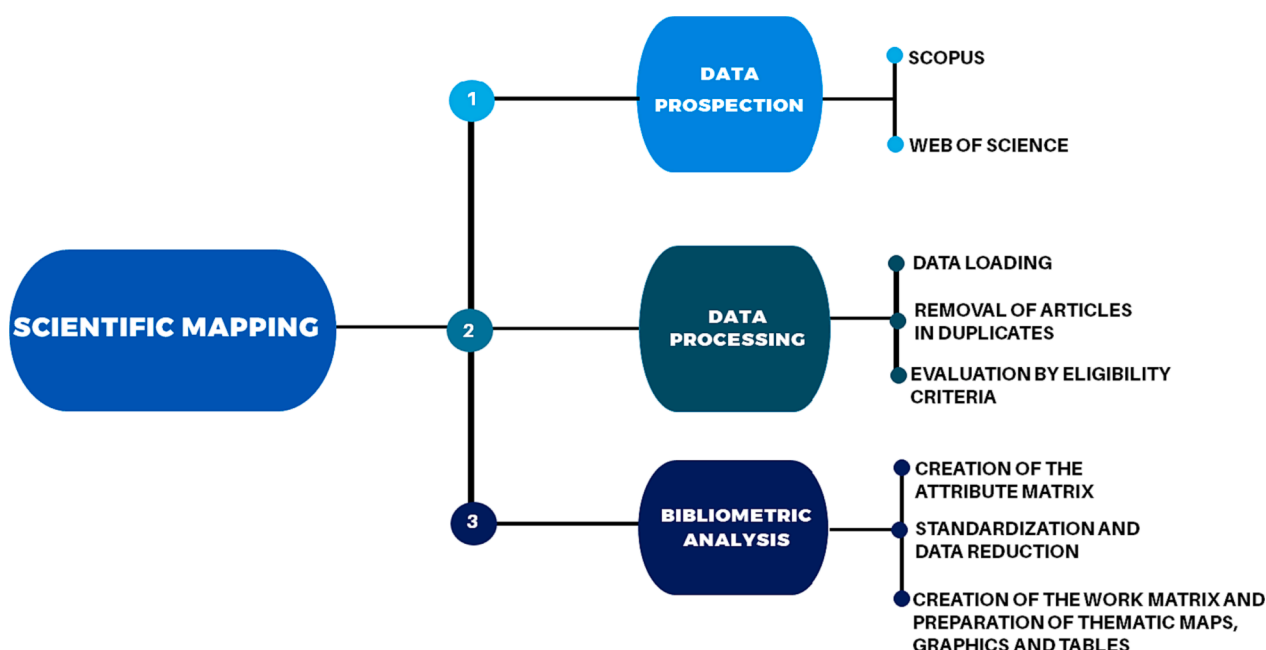


Fig. 1. Flowchart of scientific mapping: identifying key components in induced systemic resistance processes.

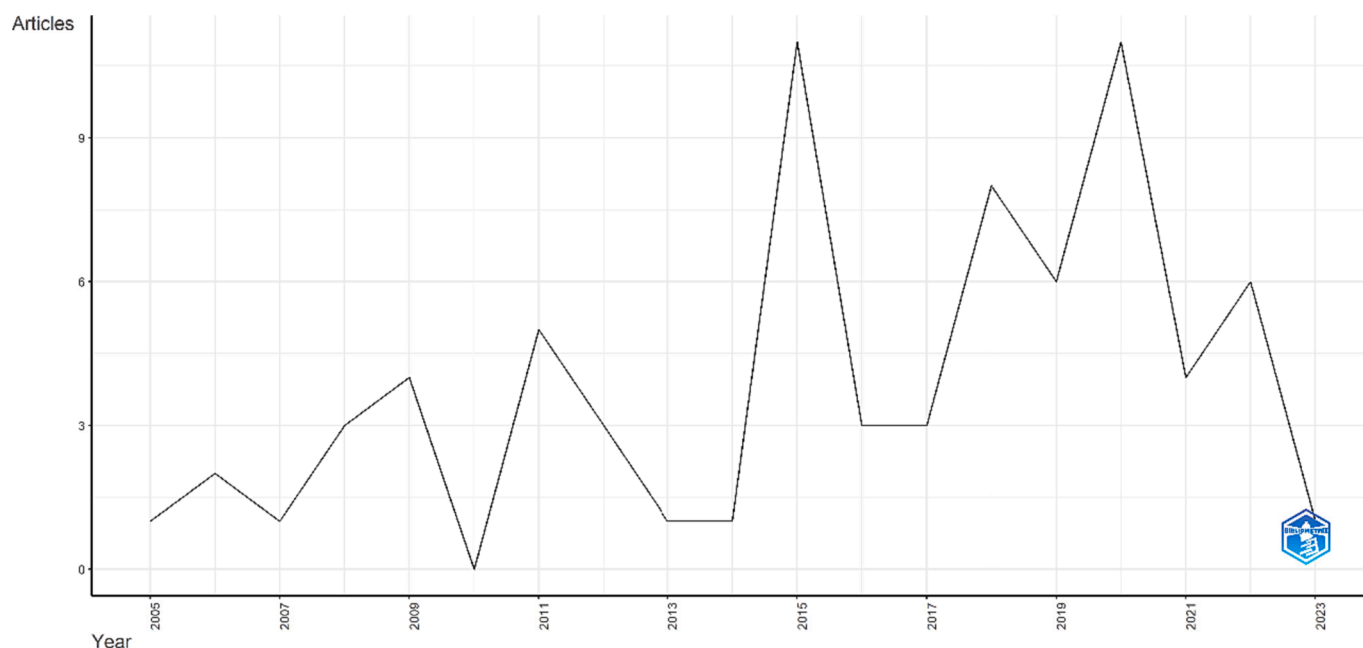


Fig. 2. Annual scientific production of studies related to induced systemic resistance.

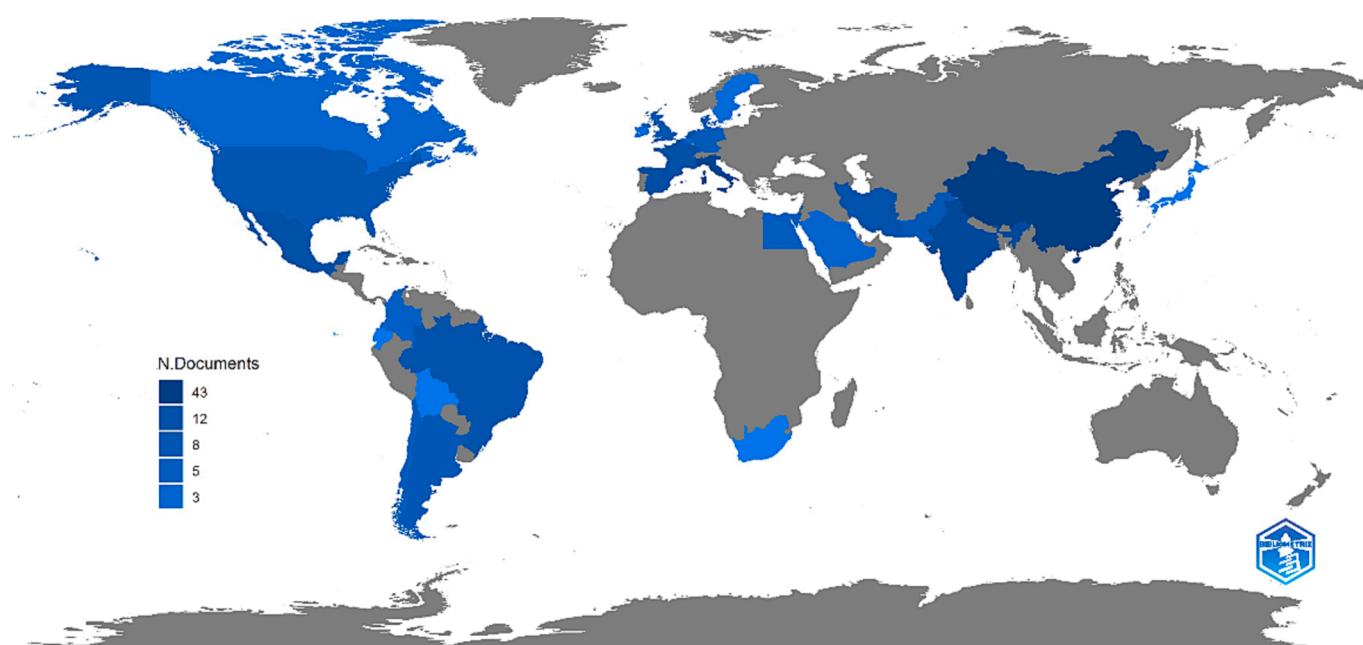


Fig. 3. Scientific production by country: top contributors to induced systemic resistance research (2005–2023).

citations were measured (Aria et al., 2020).

2.2. Social and conceptual framework

To comprehend the interconnections among authors or institutions and discern the predominant themes and trends within the realm of scientific research, an assessment was conducted on both the social and conceptual structures.

The social structure was delineated through the analysis of co-authorship networks (McCain, 1991). This analytical approach provides a visual representation of how authors or institutions engage with others in the scientific research domain. Subsequently, the collaboration network of authors and the global map of collaborations were generated,

as outlined by Aria and Cuccurullo in 2017 and Aria et al. in 2020.

Conversely, the conceptual structure illuminates the associations between concepts or words within a compilation of publications. It gauges centrality and connections with other themes, delving into the keyword field of authors (Aria and Cuccurullo, 2017; Mumu et al., 2021; Nunes et al., 2022). This evaluation employed the co-word network and multiple correspondence analysis. The structures were crafted with the assistance of the Biblioshiny platform from Bibliometrix (Aria and Cuccurullo, 2017) and VOSviewer by Van Eck and Waltman (2010).

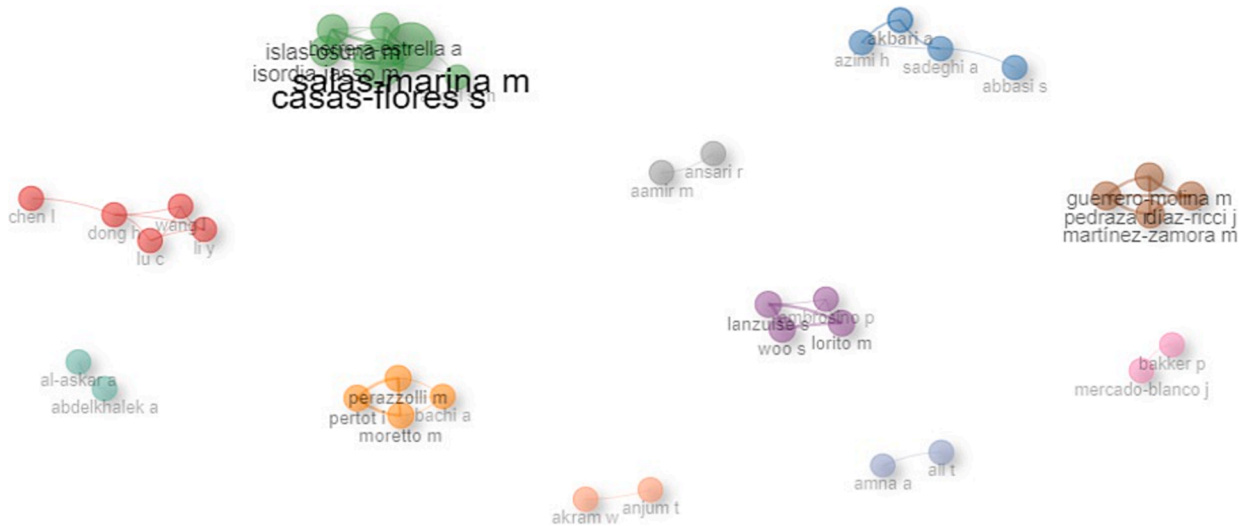


Fig. 4. Collaboration network: key contributors and networks in induced systemic resistance research.

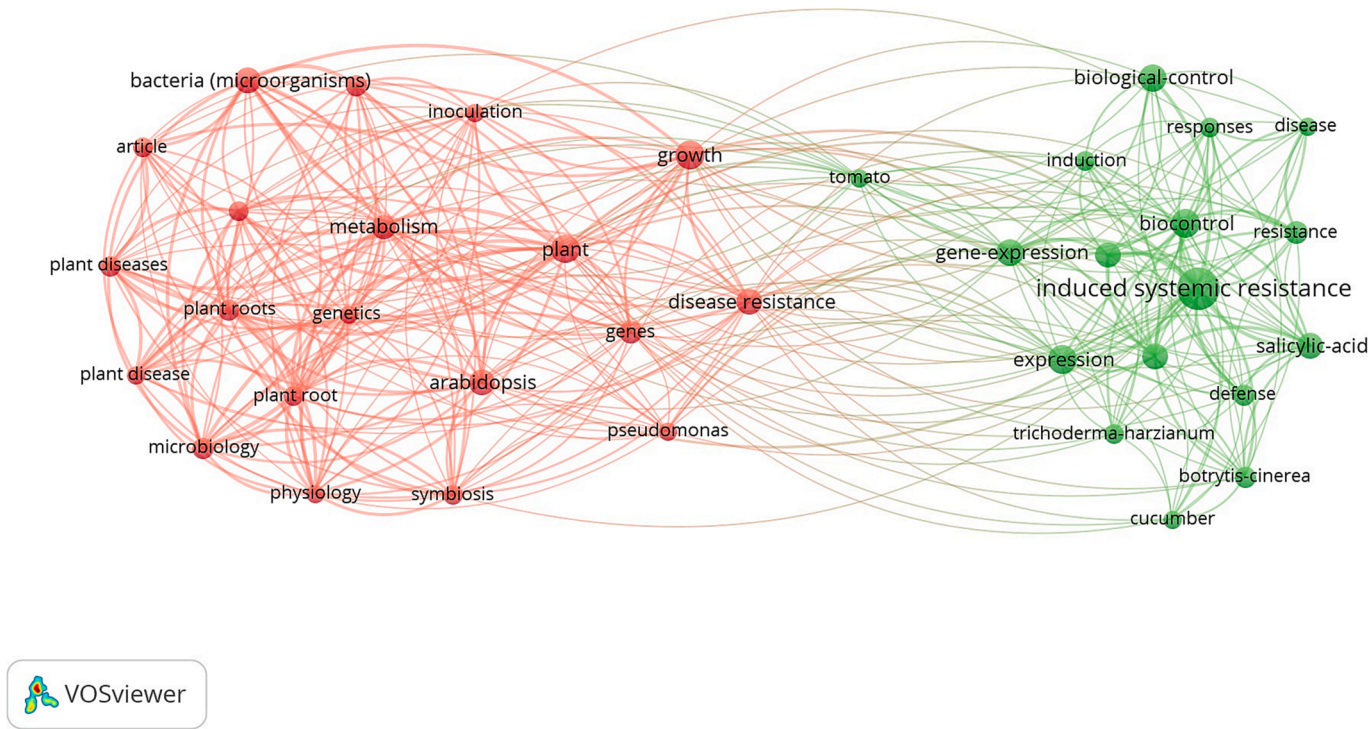


Fig. 5. Relationship between the most frequently used words in the mentioned studies related to induced systemic resistance.

2.3. Investigation of microorganisms and their interactions with gene expression and metabolites involved in plant defense systems

Using the file generated by Bibliometrix, the metadata was extracted, and a new file was created. In this file, the primary beneficial microorganisms (genus and species), plant species, and pathogens used in ISR studies were identified, along with the genes and metabolites implicated in this process. In cases where a study involved multiple species of beneficial microorganisms, pathogens, or plants, the data was treated as independent and assessed separately. Using this data, the proportion of beneficial microorganism species, plants, pathogens, expressed genes, and metabolites employed in ISR assays was calculated relative to the total number of studies. Graphs and tables were subsequently created using GraphPad Prism 8 software for data visualization and analysis.

3. Results

3.1. Bibliometrics of induced systemic resistance studies

The database search yielded a total of 136 articles. After removing 23 excluding 38 based on eligibility criteria, 75 publications remained. These publications cover a span of 18 years, with the year 2015 having the highest number of publications (Fig. 2). Authors from 29 countries contributed to publications over the course of these 18 years. The countries with the highest number of publications during this period were China (43 authors), followed by Italy (27 authors), India (20 authors), South Korea (16 authors), and Spain (13 authors) (Fig. 3). Eleven collaboration networks were identified, with Mexico (11

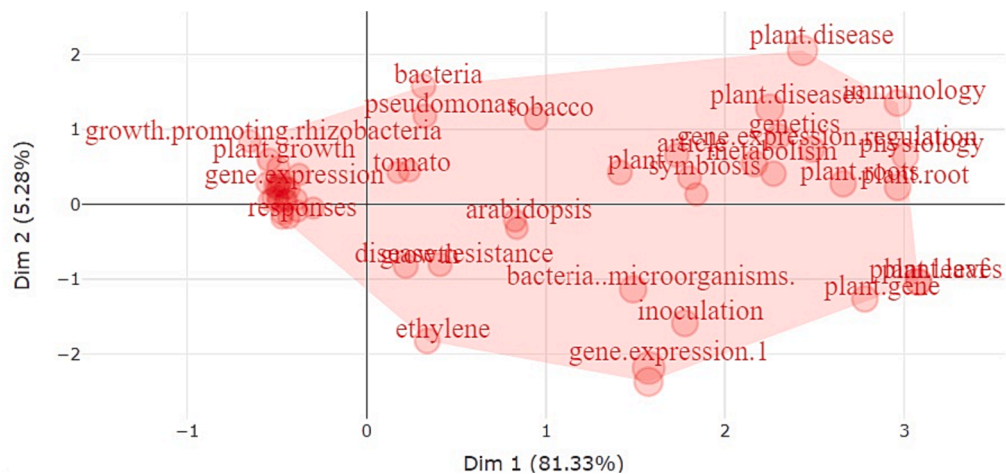


Fig. 6. Multiple correspondence analysis of the most commonly used terms in the mentioned studies related to induced systemic resistance. The results can be visualized in a scatter plot where each point represents an observation, and the distance between points reflects the dissimilarity or association between observations.

Table 1
Correlation between terms and dimensions used terms in the studies related to induced systemic resistance.

Word	Dim.1	Dim.2	Cluster	Word	Dim.1	Dim.2	Cluster
Growth.Promoting.Rhizobacteria	−0.65	0.84	1	Pseudomonas	0.32	1.18	1
Disease	−0.55	0.28	1	Bacteria	0.32	1.58	1
Plant. Growth	−0.54	0.59	1	Ethylene	0.34	−1.82	1
Rhizoctoni.solani	−0.54	0.05	1	Disease.Resistance	0.41	−0.8	1
Resistance	−0.52	0.08	1	Arabidopsis	0.83	−0.22	1
Defense	−0.51	0.24	1	Genes	0.84	−0.32	1
Induced.Systemic.Resistance	−0.5	0.21	1	Tobacco	0.94	1.15	1
Botrytis cinerea	−0.5	0.1	1	Plant	1.42	0.43	1
Biocontrol	−0.49	0.25	1	Bacteria.Microorganisms.	1.49	−1.13	1
Arabidopsis thaliana	−0.49	0.49	1	Gene.Expression.1	1.58	−2.18	1
Biological.Control	−0.49	0.04	1	Fungus	1.58	−2.37	1
Salicylic.Acid	−0.48	0.32	1	Article	1.73	0.65	1
Gene.Expression	−0.48	0.27	1	Inoculation	1.78	−1.59	1
Biosynthesis	−0.47	−0.13	1	Symbiosis	1.8	0.36	1
Rhizobacteria	−0.47	−0.18	1	Nonhuman	1.84	0.13	1
Induction	−0.45	0.22	1	Metabolism	2.17	0.54	1
Trichoderma harzianum	−0.45	0.05	1	Plant.Diseases	2.25	1.28	1
Acquired.Resistance	−0.45	0.06	1	Microbiology	2.27	0.41	1
Responses	−0.43	−0.18	1	Genetics	2.3	0.91	1
Cucumber	−0.43	0.21	1	Plant.Disease	2.43	2.06	1
Expression.	−0.39	0.07	1	Gene.Expression.Regulation	2.48	0.74	1
Defense.Responses	−0.38	0.4	1	Plant.Roots	2.66	0.27	1
Mechanisms	−0.38	−0.09	1	Plant.Gene	2.78	−1.26	1
Systemic.Resistance	−0.3	−0.05	1	Plant.Root	2.96	0.23	1
Tomato	0.17	0.43	1	Immunology	2.96	1.35	1
Growth	0.22	−0.82	1	Physiology	3.01	0.64	1
Plants	0.24	0.45	1	Plant.Leaf	3.08	−1.04	1

authors) being among the countries with the highest collaboration: Flores S., Salas Arina M, Herrera Estrella A., Isla Osuna M., Isordia Jasso M., and Angel S. (Fig. 4).

Among the most frequently used keywords, two clusters were observed (Fig. 5), both centered around the terms “metabolism” and “induced systemic resistance”. These terms were associated with other terms within their respective clusters, but not with each other. The cluster containing the term ‘metabolism’ was larger and situated further to the right. The term ‘disease resistance’ exhibited associations with numerous terms in both clusters. Similarly, the term ‘tomato’ occupied a central position between the clusters and displayed connections with terms in both clusters (Fig. 5).

The multiple correspondence analysis generated a two-dimensional plot that accounted for 86.51% of the total variability among the most frequently used words. Dimension 1 (Dim 1) represented 81.33% of this variability, while Dimension 2 (Dim 2) represented 5.28% (Fig. 6).

A multivariate analysis of the key terms and words employed in the

articles of our systematic review is present in Fig. 6. The positions of categories or groups in the plot help interpret the relationships between variables. Categories or groups that are close together are more strongly associated, while those farther apart are less associated. In our results, we describe the primary terms and words based on this analysis and their relationship with the dimensions. A unified cluster emerged, encompassing terms such as ‘biosynthesis,’ ‘rhizobacteria,’ ‘mechanism,’ ‘systemic resistance,’ and ‘responses,’ all of which exhibited minimal and negative correlation with both dimensions. Conversely, the terms “plant disease,” “plant diseases,” and “immunology” had a positive correlation above 1 for both dimensions (Table 1).

3.2. Characteristics of studies on induced systemic resistance

Twenty-four genera of beneficial microorganisms were utilized in ISR studies (Fig. 7).

The genera *Trichoderma*, *Bacillus*, and *Pseudomonas* were extensively

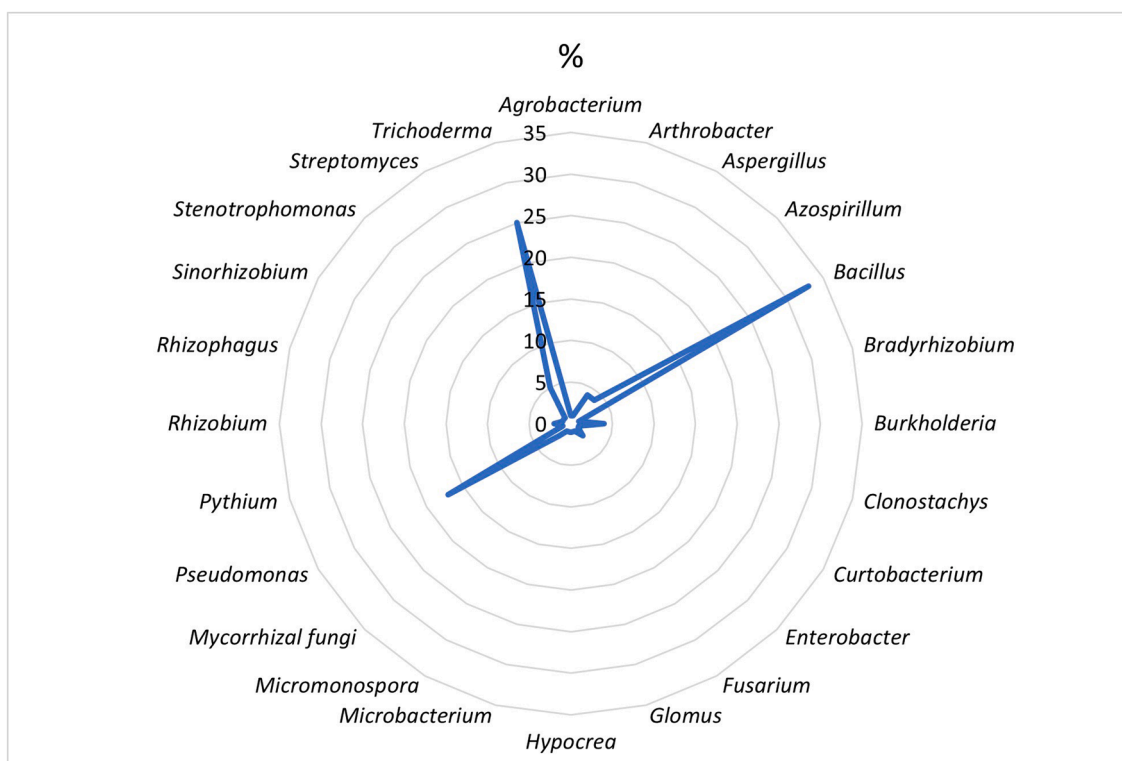


Fig. 7. Genera (%) of microorganisms employed in induced systemic resistance studies.

researched, representing 25%, 33%, and 17% of the publications, respectively. The remaining genera were featured in fewer than 5% of the studies.

Seven species of *Trichoderma* were utilized in ISR studies, with *Trichoderma harzianum* Rifai appearing in 35% of the cases, while *Trichoderma asperelloides* Samuels and *Trichoderma koningiopsis* C.P. Kubicek were present in only 5% of the studies (Fig. 8).

Within the *Bacillus* genus, *Bacillus subtilis* (Ehrenberg, 1835) Cohn, 1872 was the most frequently investigated species, featuring in 30% of the publications, followed by *Bacillus amyloliquefaciens* Priest et al., 1987 (19%) and *Bacillus velezensis* Ruiz-Garcia et al., 2005 (19%). Within the *Pseudomonas* genus, 38% of the studies did not specify the species, while among those that did, *P. fluorescens* was identified in 23% of the works. The genera *Trichoderma* and *Bacillus* have demonstrated antagonistic capabilities against a broad spectrum of pathogens. When in contact with plants, they induce changes in gene expression and produce substances that, upon contact with plant tissues, modulate the expression of genes related to promoting growth and inducing ISR (Cardoza et al., 2015; Lin et al., 2020; Salas-Marina et al., 2015).

A total of 25 plant species were included in the prospecting meta-data. Among these, *Solanum lycopersicum* L. (24%) was the most frequently studied species in ISR research, followed by *Arabidopsis thaliana* (L.) Heynh. (17%), *Cucumis sativus* L. (11%), and *Vitis vinifera* L. (7%). The remaining species were present in less than 5% of the articles (Fig. 9).

Regarding the pathogens included in the evaluated pathosystems, four species accounted for more than 50% of the studies. These are: *Botrytis cinerea* Pers. (19%), *Pseudomonas syringae* van Hall, 1902 (14%), *Rhizoctonia solani* J.G.Kuhn (12%), and *Fusarium oxysporum* Schltdl. (7%). The remaining pathogens represent 48% of the publications.

Over the course of 18 years, 143 plant genes have been correlated with induced systemic resistance (Table 2). These genes are related to the synthesis of hormones such as ethylene, jasmonic acid, and salicylic acid, as well as the encoding of scavenger enzymes, proteins related to pathogenicity, and biotic stress response proteins.

On the other hand, few studies have evaluated the expression of microbial genes that are being regulated during ISR. Only seven genes from beneficial microorganisms have been related to ISR (Table 3), with three genes expressed by *Trichoderma* species, three genes expressed by *Bacillus cereus*, and two genes expressed by *Enterobacter intermedium* Izard et al., 1980.

Hormones, enzymes, proteins, and reactive oxygen species were the main metabolites associated with ISR, of which salicylic acid (27%), ethylene (25%), peroxidase (24%), jasmonic acid (24%), and chitinase (19%) were the most commonly present in these studies, while the remaining metabolites were present in less than 10% (Fig. 10).

4. Discussion

Microorganisms such as viruses, bacteria, and fungi have the ability to combat phytopathogens and replace the use of chemical agents. They activate plant defense mechanisms and control disease incidence by acting through elicitors (Zehra et al., 2021).

Elicitors are endogenous or exogenous substances produced by plants themselves, beneficial microorganisms, and pathogens, which are responsible for triggering physiological responses to biotic stress, such as induced systemic resistance (Barka et al., 2022; del Carmen Orozco-Mosqueda et al., 2023). Induced systemic resistance is associated with a series of defense responses, including defense proteins, salicylic acid, and hormone-dependent signaling pathways. Although the exact mechanism of induced resistance is not yet fully understood, it is known to be initiated by microbial-associated molecular patterns that bind to plant pattern recognition receptors and trigger defensive responses within minutes (Pršić and Ongena, 2020; Rahman et al., 2015).

In the present review, it was observed that even in the absence of a pathogen, beneficial microorganisms activated genes in plants related to jasmonic acid, ethylene, and scavenger enzymes (Elías et al., 2018; Gómez-Lama Cabanás et al., 2022; Sáenz-Mata et al., 2014). Indicating that there is a plant response to infection by beneficial microorganisms, however, this response seems to be interrupted in phase II, which

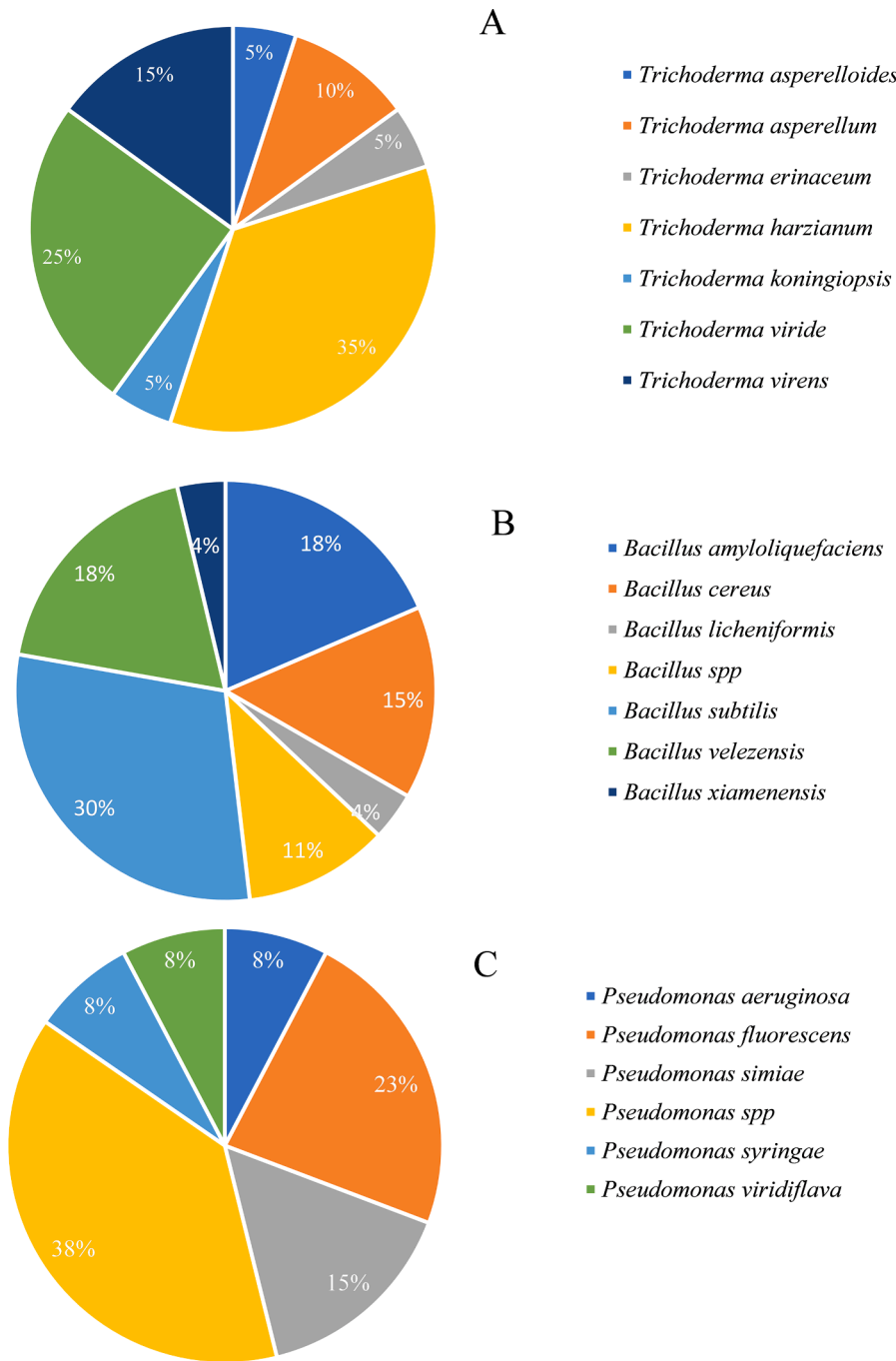


Fig. 8. Main species of beneficial microorganisms employed in studies evaluating induced systemic resistance. A = *Trichoderma*, B = *Bacillus*, C = *Pseudomonas*.

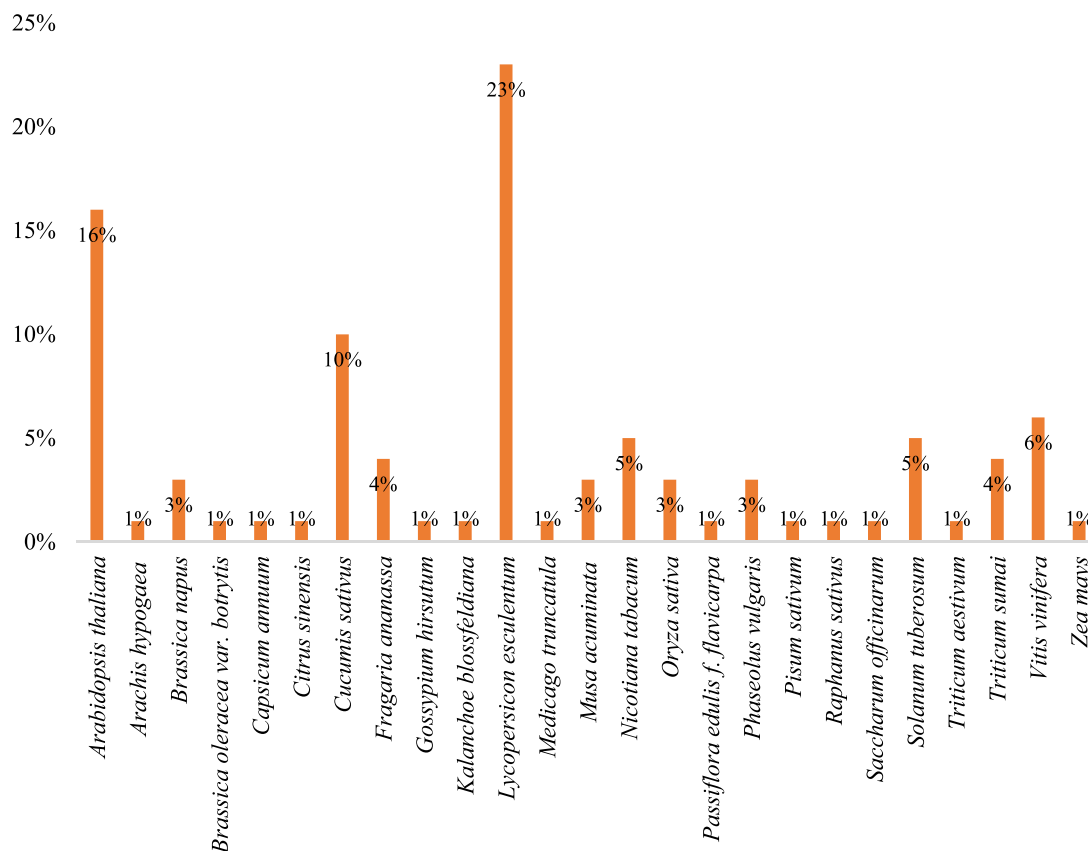


Fig. 9. Most used plant species in studies of induced systemic resistance.

involves the effector molecules (Malik et al., 2020). Early recognition of beneficial microorganisms by plants, along with signal transduction, plays important roles in inducing systemic resistance. Additionally, non-coding RNAs may be involved in the perception and recognition of plants to both beneficial and harmful microorganisms, contributing to plant immunity. Consequently, non-coding RNAs can be key in unraveling the mechanisms underlying induced systemic resistance (Huang et al., 2023; Zhou et al., 2021), however, there are still limited studies investigating the role of non-coding RNAs in plant immunity (Sharma et al., 2022).

Although beneficial microorganisms have evolved to minimize the activation of the host plant's immune system, there is still an urgent need for detailed research on the balance between efficient recognition and the strength of the host immune response. Genes and transcription factors play a complex role in plant defense response, with interactions between signaling pathways involving salicylic acid, jasmonic acid, ethylene, and MAPK. Genome-wide miRNA profiling analysis and subsequent functional verification are important for a better understanding of these mechanisms and for the development of strategies for plant disease and pest control. RNA interference technology shows promise in this regard. These advancements are crucial for establishing an efficient symbiosis between beneficial microorganisms and host plants, driving research in sustainable agriculture (Yu et al., 2022).

Several natural and recombinant microorganisms, such as *Bacillus*, *Pseudomonas*, and *Trichoderma*, are commercially available as biological control agents. A comprehensive understanding of these agents and their interactions at cellular and molecular levels is crucial for identifying effective and environmentally sustainable biological agents (Zehra et al., 2021).

Trichoderma is a versatile and opportunistic fungal genus that provides significant benefits in agriculture. It acts as a direct biological control agent against phytopathogens by competing and antagonizing

other microorganisms in the rhizosphere (Ferreira and Musumeci, 2021; Sumida et al., 2018). In addition, *Trichoderma* establishes a beneficial association with plants, promoting their growth and protection. Its ability to induce defense responses in plants against biotic and abiotic stresses, as well as its capacity to activate transcriptional memory, has sparked significant scientific interest (Molinari and Leonetti, 2019; Segarra et al., 2009). The diversity of *Trichoderma* and its multiple applications as biological control agents, bio-stimulants, and bio-fertilizers have been driving research in this field (Greco et al., 2012; Kashyap et al., 2020).

However, the development of innovative products based on *Trichoderma* faces challenges due to restrictions in registration and authorization procedures. These restrictions range from inflexible terminology to limited communication between researchers and policymakers. Despite this, it is important to continue exploring the potential of *Trichoderma* as a beneficial microorganism for sustainable agriculture, aligning with legislative policies that seek alternatives to synthetic chemicals (Lahlali et al., 2022; Mawar et al., 2021).

Multidisciplinary investigations are crucial for a comprehensive understanding of the properties of *Trichoderma*. By maximizing the benefits of this green fungus, we can promote safe and eco-sustainable agriculture, contributing to a better quality of life and the achievement of the Sustainable Development Goals (SDGs) set by the United Nations (Woo et al., 2023).

Just like *Trichoderma*, plant growth-promoting rhizobacteria (PGPR) are beneficial microorganisms that inhabit the rhizosphere of plants. They play a crucial role in promoting plant growth and enhancing resistance against biotic and abiotic stresses. However, there are still gaps in our knowledge regarding the chemical communications between plants and microorganisms in the rhizosphere, as well as the biochemical implications of these interactions on the plant metabolome (Shelef et al., 2019).

Table 2

Genes, expression, beneficial microorganism, and pathogens involved in induced systemic resistance.

Gene/Expression	Beneficial microorganism	Patogen
LOX - Lipooxygenase enzyme in plants	<i>Trichoderma asperellum</i> , <i>Bacillus licheniformis</i> , <i>B. cereus</i> , <i>B. subtilis</i> , <i>T. asperelloides</i> , <i>T. harzianum</i> , <i>Trichoderma atroviride</i> , <i>Pseudomonas viridiflava</i> , <i>Burkholderia phytofirmans</i> , <i>Aspergillus ustus</i> , <i>Fusarium esquiseti</i>	<i>P. syringae</i> pv <i>tomato</i> , <i>Hyaloperonospora parasitica</i> , <i>Plectosphaera cucumerina</i> , <i>Botrytis cinerea</i> , <i>P. syringae</i> , <i>Fusarium oxysporum</i> , <i>Cucumovirus</i> , <i>Bromoviridae</i> , <i>Xanthomonas campestris</i> , <i>Sclerotinia sclerotiorum</i> , <i>Leptosphaeria maculans</i> , <i>Podosphaera xanthii</i> , <i>Rhizoctonia solani</i>
CHI - Enzyme chitinase in plants	<i>T. virens</i> , <i>T. atroviride</i> , <i>T. harzianum</i> , <i>B. amyloliquefaciens</i> , <i>P. syringae</i> , <i>Pseudomonas</i> sp., <i>Burkholderia phytofirmans</i>	<i>B. cinerea</i> , <i>Alternaria solani</i> , <i>P. syringae</i> , <i>Plasmopara viticola</i> , <i>Penicillium digitatum</i> , <i>F. oxysporum</i> , <i>Erysiphe cichoracearum</i> , <i>P. xanthii</i>
AOS - Acid hydroperoxide synthase enzyme in plants	<i>P. syringae</i> , <i>P. simiae</i>	<i>P. digitatum</i>
GPX1 - Enzyme glutathione peroxidase	<i>P. syringae</i> , <i>T. erinaceum</i>	<i>P. digitatum</i> , <i>F. oxysporum</i>
CHI9 - 30 kD basic intracellular chitinase	<i>T. harzianum</i> , <i>T. atroviride</i> , <i>T. virens</i>	<i>B. cinerea</i> , <i>A. Solani</i> , <i>Podosphaera xanthii</i>
PR-5x - PR-5 proteins. These proteins are homologous to thaumatin	<i>T. virens</i> , <i>T. atroviride</i> , <i>B. cereus</i> , <i>B. subtilis</i> , <i>Glomus</i> sp., <i>Streptomyces</i> sp.	<i>B. cinerea</i> , <i>Alternaria Solani</i>
alfa-DOX1 - Alpha-dioxygenase	<i>T. virens</i> , <i>T. atroviride</i>	<i>B. cinerea</i> , <i>A. solani</i> , <i>Pythium</i> sp., <i>Meloidogyne incognita</i> , <i>B. cinerea</i> , <i>A. Solani</i>
cevi16 - Peroxidase		
TLRP - Proteins rich in tyrosine and lysine		
LOC101262163 - Actin-7-like proteins		
emb1187 - Phospholipid biosynthesis	<i>T. atroviride</i>	–
AT4G14370 - Disease resistance protein family		
WRKY54 - DNA binding protein WRKY 54		
MYB114 - Myb domain protein 114		
AtWRKY - WRKY DNA binding proteins		
SOD - Superoxide dismutase, which destroys radicals produced within cells that are toxic	<i>B. amyloliquefaciens</i> , <i>T. asperellum</i> , <i>T. erinaceum</i> , <i>T. harzianum</i>	<i>X. oryzae</i> pv. <i>Oryzae</i> , <i>Cucumovirus</i> , <i>bromoviridae</i> , <i>F. oxysporum</i> , <i>Cucumber mosaic virus</i> , <i>P. xanthii</i> , <i>B. cinerea</i>
Erf1 - Ethylene response factor 1	<i>T. harzianum</i>	
ERF - Acts in the ethylene signaling pathway	<i>T. harzianum</i> , <i>Pseudomonas</i> spp.	<i>Phytophthora capsici</i> , <i>P. viticola</i> , <i>R. solani</i>
LOC10258890 - FAMA transcription factor	<i>T. harzianum</i>	<i>P. viticola</i>
ACS9 - The enzyme aminocyclopropane-1-carboxylate synthase catalyzes the conversion of S-adenosyl-L-methionine to 1-amino-cyclopropane-1-carboxylate, which is a precursor of ethylene.	<i>T. asperelloides</i>	<i>Pseudomonas syringae</i>
PR - Protein related to pathogenesis	<i>T. harzianum</i> , <i>A. asperelloides</i> , <i>B. velezensis</i> , <i>B. amyloliquefaciens</i> , <i>P.</i>	<i>P. syringae</i> , <i>P. capsici</i> , <i>P. xanthii</i> , <i>Erysiphe cichoracearum</i> ,

Table 2 (continued)

Gene/Expression	Beneficial microorganism	Patogen
	<i>simiae</i> , <i>A. terreus</i> , <i>B. phytofirmans</i> , <i>Pythium oligandrum</i> , <i>A. ustus</i> , <i>Azospirillum lipoferum</i> , <i>A. spinulosporus</i> , <i>Pseudomonas</i> sp., <i>F. esquiseti</i> , <i>P. viridiflava</i> , <i>Streptomyces</i> sp., <i>Rhizobium radiobacter</i> , <i>T. atroviride</i> , <i>Micromonospora</i> sp.	<i>Neofusicoccum parvum</i> , <i>B. cinerea</i> , <i>Hyaloperonospora parasitica</i> , <i>Plectosphaera cucumerina</i> , <i>Pythium</i> spp., <i>F. oxysporum</i> , <i>Ralstonia solanacearum</i> , <i>A. solani</i> , <i>P. viticola</i> , <i>Xanthomonas oryzae</i> pv. <i>Oryzae</i> , <i>Cucumovirus bromoviridae</i> , <i>X. campestris</i> , <i>S. sclerotiorum</i> , <i>Leptosphaeria maculans</i> , <i>B. cinerea</i> , <i>P. syringae</i>
PIN - Jasmonic acid	<i>T. harzianum</i> , <i>B. phytofirmans</i> , <i>A. brasilense</i>	–
etr1 , ers1 , ein4 - Ethylene receptors		
aco1 - Aconitase that may play a role in the oxidative stress response		
CAT - Encodes the enzyme catalase		
APXc - Cytosolic ascorbate peroxidase		
FLS2 - Flagellin-sensitive receptor		
AFR1 - Defense regulatory protein kinase	<i>Harpin</i> of <i>Xanthomonas oryzae</i> pv. <i>oryzicola</i>	<i>X. oryzae</i> pv. <i>oryzicola</i>
COL - Constant-type protein	<i>T. harzianum</i> , <i>P. simiae</i>	<i>P. viticola</i>
NPR - Salicylic acid-mediated regulatory protein and confers resistance to pathogens	<i>T. asperellum</i> , <i>B. amyloliquefaciens</i> , <i>R. radiobacter</i> , <i>P. simiae</i>	<i>X. oryzae</i> pv. <i>oryzicola</i> , <i>P. syringae</i> , <i>P. cucumerina</i> , <i>E. cichoracearum</i> , <i>R. radiobacter</i> , <i>T. atroviride</i> , <i>B. phytofirmans</i> , <i>P. syringae</i>
PDF 1.2 - Plant defensin that is responsive to ethylene and jasmonic acid	<i>A. ustus</i> , <i>B. velezensis</i> , <i>B. Subtilis</i> , <i>B. Amyloliquefaciens</i>	
JAR1-1 - Indole-3-acetic acid starch synthase	<i>A. terreus</i> , <i>R. radiobacter</i>	
JIN1 - MYC-related transcriptional activator and regulates several jasmonic acid-related functions	<i>R. radiobacter</i>	
VSP2 - Vegetative storage protein and is induced in response to jasmonic acid		
EDS16 - Protein with isochlorismate synthase activity, involved in the production of salicylic acid		
ASPR1 - Protein from the aspartyl protease Family		
ATPCA - CA peroxidase, may be involved in hydrogen peroxide generation during plant defense response	<i>A. ustus</i> , <i>T. atroviride</i>	<i>B. cinerea</i> , <i>P. syringae</i>
PAD3 - Terpenoid phytoalexin pathway		
ET - Ethylene response factor	<i>B. subtilis</i>	<i>R. solani</i>
XTH - Protein hydrolase 7		
HSR203J - Idol signaling pathway	<i>P. oligandrum</i>	<i>Neofusicoccum parvum</i>
GST2 - Regulating redox status		
CHORS2 - Idol signaling pathway		
CAGT - Cell wall reinforcement		
HQT - Hidroxicinamoyl CoA quinato transferase	<i>B. valezensis</i>	<i>F. oxysporum</i>

(continued on next page)

Table 2 (continued)

Gene/Expression	Beneficial microorganism	Patogen
IRT 1 -Protein that transports iron	<i>P. simiae</i>	<i>P. aeruginosa</i>
MYB72 -Protein belonging to the R2R3 transcription factor gene family, which are involved in induced systemic resistance		
NAC -Proteins of the Nac family, which are involved in stress responses	<i>B. amyloliquefaciens</i>	<i>R. solani</i>
MADS -RIN transcription factor, involved in reprogramming plant transcription under stress		
ASA1 -Jasmonic acid/ethylene-mediated defense	<i>P. simiae</i>	–
ICS1 -Ischorismate synthase		
PPO -Polyphenol oxidase	<i>T. harzianum</i> , <i>B. amyloliquefaciens</i> , <i>P. simiae</i>	<i>P. viticola</i> , <i>E. cichoracearum</i>
APX -L-ascorbate peroxidase	<i>T. harzianum</i> , <i>P. simiae</i>	<i>Cucumber mosaic virus</i>
EDS1 -Protein of the alpha/beta hydrolases superfamily, which is a component of R gene-mediated disease resistance	<i>P. simiae</i>	–
JMT -Jasmonic acid carboxyl methyltransferase, this enzyme catalyzes the reaction to form methyl jasmonate from jasmonic acid		
JAZ1 -Protein 1 of the jasmonate-zim domain, an enzyme involved in jamonate signaling	<i>B. phytofirmans</i>	<i>B. cinerea</i>
Solyc01g091170.3 -Arginase 2, an enzyme involved in the metabolism of arginine for polyamine biosynthesis	<i>B. velezensis</i>	
Solyc08g076970.3 -Acetyl carnitine deacetylase, an enzyme involved in nitrate metabolism for polyamine biosynthesis		
pi2 -Peptidyl-prolyl cis-trans isomerase CYP95	<i>T. harzianum</i>	
pi3 -Phosphatidylinositol 4-kinase gamma 7		
Pti4, pti5 -Trans action factors of PR genes		
TOM51 -Actin type 7		
TOM52 -Actin		
STKR -Serine/threonine kinase receptor		<i>P. viticola</i>
SAMT -S-adenosyl-L-methionine:benzoic acid/salicylic acid 3 carboxyl methyltransferase 3		<i>B. cinerea</i>

The rhizosphere microbiome and its metabolites interact with plants, contributing to their health through hormonal modulation, nutrient provision, and pathogen suppression. Chemical dialogues between plants and the rhizosphere microbiome, mediated by plant volatile organic compounds (VOCs) and microbial volatile organic compounds (MVOCs), play a role in plant communication and defense (Howard

Table 3

Genes expressed by beneficial microorganisms during ISR.

Genes	Microorganism
<i>ptsG</i>	Transport and metabolism of sugars, particularly glucose, in bacterial cells. It highlights the involvement of a transport protein called IIAGlc, which is part of the phosphotransferase system (PTS) responsible for facilitating the uptake of glucose from the environment. <i>Bacillus cereus</i>
<i>ptsHI</i>	<i>ptsH</i> gene encodes the HPr protein, while the <i>ptsI</i> gene encodes the EI enzyme. These proteins play crucial roles in the transport and metabolism of sugars in bacterial cells. They are responsible for the uptake and phosphorylation of sugars, and they also participate in regulating and transmitting metabolic signals related to sugar uptake and metabolism processes. <i>B. cereus</i>
<i>ptsGpromoter</i>	Involved in the expression of the <i>ptsG</i> gene, affecting the transport and metabolism of sugars in bacterial cells. <i>B. cereus</i>
<i>TRI4</i>	Encode Trichodiene oxygenase <i>Trichoderma harzianum</i>
<i>epl1</i> and <i>sml1</i>	Encodes plant-like response eliciting proteins <i>T. virens</i> <i>T. atroviride</i>
<i>pqqA</i> and <i>pqqB</i>	Genes that are involved in coding for pyrroloquinoline quinone. <i>E. intermedium</i>

et al., 2022; Kai et al., 2016). Indeed, the communication that occurs through microbial volatile organic compounds (MVOCs) and plants directly influences the expression of genes related to induced systemic resistance (ISR). The MVOCs released by beneficial microorganisms in the rhizosphere can trigger specific signaling pathways in plants, leading to the activation of defense-related genes and the induction of ISR. This communication plays a vital role in enhancing the plant's ability to respond to pathogen attacks and other biotic stresses (Kong et al., 2018). Understanding the mechanisms of MVOCs as weapons against plant pathogens and exploring their potential as environmentally friendly biocontrol solutions is essential for the development of intelligent biological formulations (Thankappan et al., 2022).

PGPRs can reduce phytopathogenic infestations and increase crop yield, not only through MVOCs but also through direct mechanisms such as the production of antimicrobial metabolites, and indirect mechanisms by stimulating plant immune responses. Although there are challenges to overcome for the large-scale application of PGPRs, the development of properly formulated inoculants can provide a holistic approach to improving plant health and increasing crop productivity (Khoshru et al., 2023). Among the PGPR genera, the genus *Bacillus* has stood out for presenting different functionalities in its interaction with plants (Blake et al., 2021; Dame et al., 2021; Miljaković et al., 2020). The genus *Bacillus* is present in the soil and plant rhizosphere and plays a significant role in protecting plants against pathogens through induced systemic resistance (ISR) (Abdelkhalek et al., 2020; Kang et al., 2019; Rahman et al., 2015). However, the full potential of the *Bacillus* genus still needs to be explored, and its transfer to practical applications requires more attention.

Therefore, microbiome engineering has been studied as an approach to promote sustainability in agriculture and achieve the Sustainable Development Goals. This study highlights the potential of the plant microbiome and its contribution to sustainable agriculture and sustainable development (Sonowal, et al., 2023).

5. Conclusion

Beneficial microorganisms induce systemic resistance in plants. Among the genera of beneficial microorganisms, *Trichoderma*, *Bacillus*, and *Pseudomonas* stand out. When these species encounter plants, they alter gene expression, resulting in the production of substances that,

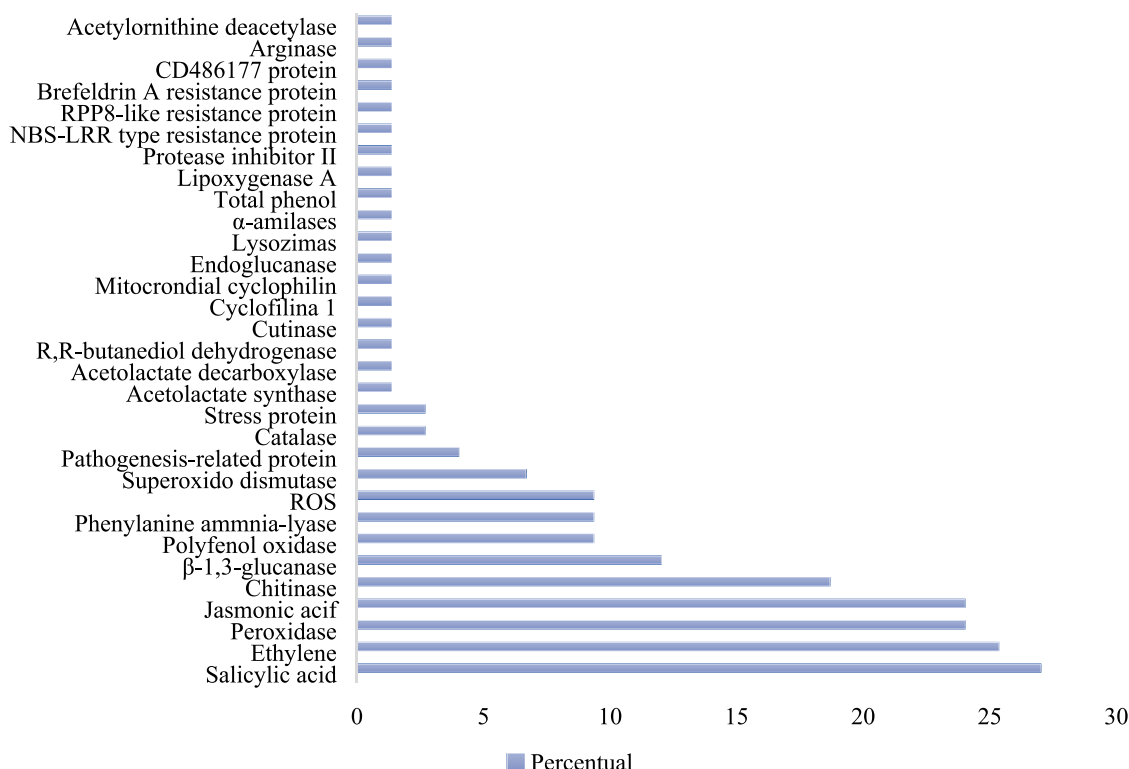


Fig. 10. Assessment of Plant Defense Metabolites in Induced Systemic Resistance Studies.

upon contact with plant cells, stimulate the expression of genes responsible for signaling and producing proteins and enzymes involved in the signaling of jasmonic acid, salicylic acid, ethylene, as well as metabolites that reduce disease incidence.

CRedit authorship contribution statement

Matheus Emmanuel Oliveira Vieira: Conceptualization, Data curation, Formal analysis, Writing – original draft. **Valdinete Vieira Nunes:** Methodology, Validation. **Crislaine Costa Calazans:** Methodology, Validation. **Renata Silva-Mann:** Project administration, Supervision, Validation, Writing – review & editing.

Declaration of Competing Interest

There are no competing interests associated with this article.

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Ethical approval

This article does not contain any studies with human participants or animals performed by any of the authors.

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