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Induced Resistance in Fruit and Vegetable Enhancing Host Defence to Curve Post-harvest Diseases

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Induced resistance (IR) is an emerging, environmentally friendly strategy to manage post-harvest diseases in fruits and vegetables by enhancing the plant’s innate immune system. This approach leverages the plant's natural defense mechanisms, including the activation of defense-related enzymes like chitinases, glucanases, and peroxidases, accumulation of secondary metabolites such as phytoalexins and phenolics, and the strengthening of cell walls to prevent pathogen invasion. Additionally, the production of reactive oxygen species (ROS) plays a crucial role in both signaling and direct pathogen inhibition. Despite its potential, the effectiveness of IR varies across different crops and pathogens, and its success is heavily influenced by environmental factors, such as humidity, temperature, and light. There are also concerns regarding possible trade-offs, such as reduced yield or changes in fruit quality due to the diversion of energy towards defense responses. However, the integration of IR with other disease management strategies, including the use of biological control agents and conventional fungicides, has shown promising results in reducing post-harvest losses. Case studies in fruits like apples, tomatoes, and citrus, as well as vegetables like potatoes and peppers, demonstrate the practical applications of IR in commercial agriculture. Advances in genetic engineering are opening new pathways for enhancing IR by manipulating key genes involved in defense pathways, while new formulations and precision agriculture technologies offer greater control and efficiency in IR applications. These innovations, along with optimized post-harvest handling and storage practices, hold the potential to make IR a more reliable and sustainable solution for managing post-harvest diseases. However, ongoing research is necessary to address the variability in effectiveness and to explore long-term sustainability, especially as pathogens evolve and environmental conditions change. Induced resistance, when integrated with a comprehensive disease management approach, offers a significant step forward in reducing post-harvest losses and improving food security globally.

Keywords: Induced resistance; post-harvest; pathogens; biocontrol; phytoalexins; genetic engineering.

1. INTRODUCTION

A. Fruits and Vegetables in Global Agriculture

Fruits and vegetables are fundamental components of human nutrition, contributing essential vitamins, minerals, and dietary fiber that are crucial for health. Globally, these crops are cultivated across diverse agro-climatic regions, offering significant economic value to both local farmers and international markets [1]. According to the Food and Agriculture Organization (FAO), fruits and vegetables account for approximately 21% of global agricultural production, with over 2 billion metric tons produced annuallytion to their economic significance, fruits and vegetables also play an important role in ensuring food security and promoting sustainable agricultural practices. The demand for fruits and vegetables is increasing due to rising population growth and a greater awareness of their health benefits. However, this sector faces significant challenges in terms of post-harvest losses, leading to food wastage and economic detriment.

B. Challenges Posed by Post-Harvest Diseases

Post-harvest diseases are one of the most severe challenges facing the fruit and vegetable industry, resulting in losses of up to 30% in some regions, with fungi and bacteria as the primary pathogens responsible for spoilage [2]. These ffect both the quantity and quality of produce, leading to significant economic losses and decreased market value. Pathogens such as *Botrytis cinerea*, *Penicillium spp.*, and *Erwinia spp.* often infect fruits and vegetables during storage and transportation, exacerbating losses during the post-harvest phase . In developing d storage and advanced handling technologies are limited, these losses are even more pronounced. Post-harvest diseases not only diminish the shelf life of products but also pose health risks to consumers, as decayed products can harbor harmful toxins produced by pathogenic organisms.

C. Role of Induced Resistancating Post-Harvest Losses

Induced resistance (IR) represents a promising approach to reducing post-harvest diseases in fruits and vegetables. This natural plant defense mechanism is activated in response to external stimuli, such as pathogen attack, and leads to the production of defense-related enzymes, secondary metabolites, and structural barriers. The concept of induced resistance has gaining attention as an environmentally friendly and sustainable method for enhancing crop protection without relying solely on chemical pesticides. By priming the plant's innate immune system, IR enables fruits and vegetables to defend themselves against a wide range of pathogens during both pre-harvest and post-harvest stages [3]. Recent studies have shown that systemic acquired reSAR) and induced systemic resistance (ISR) are the two primary pathways through which IR is activated. SAR is typically triggered by the accumulation of salicylic acid, while ISR is mediated by jasmonic acid and ethylene signaling pathways. This dual activation of plant defense mechanisms provides brum resistance against fungal, bacterial, and viral pathogens, making IR a valuable tool for reducing post-harvest spoilage.

D. Objectives and Scope of the Review

The objective of this review ate the role of induced resistance in mitigating post-harvest diseases in fruits and vegetables. This will involve an in-depth analysis of the mechanisms underlying induced resistance, its practical applications in commercial agriculture, and the challenges associated with its implementation. The review will also explore case studies of successful induced resistance interventions in fruit and vegetable crops, highlighting the role of biocontrol agents, chemical inducers, and physical methods in enhancing post-harvest disease resistance. Additionally, the potential limitations and future perspectives of using induced resistance as a sustainable strategy for post-harvest disease management will be discussed [4]. The scope of this review will encompass the latest research findings in the field of induced resistance, with a focus on integrating these findings into practical solutions that can be applied at the commercial level to reduce post-harvest losses.

2. POST-HARVEST DISEASES IN FRUITS AND VEGETABLES

A. Common Pathogens Responsible for Post-Harvest Diseases

Post-harvest diseases are a significant factor contributing to the deterioration of fruits and vegetables during storage and transportation. These diseases are predominantly caused by fungal, bacterial, and viral pathogens that invade the produce during harvest, handling, or storage, resulting in considerable economic losses and reduced quality (Table 1). Pathogen invasion is often influenced by external factors such as temperature, humidity, and physical damage to the produce, leading to accelerated spoilage [5].

1. Fungal Pathogens (e.g., *Botrytis cinerea*, *Penicillium spp.*)

Fungal pathogens are among the most common culprits of post-harvest spoilage in fruits and vegetables. *Botrytis cinerea*, commonly known as gray mold, is a highly destructive pathogen affecting a wide range of fruits, including strawberries, grapes, and tomatoes. It typically invades through wounds or natural openings and thrives in humid, cool storage conditions, leading to soft rot and water-soaked lesions. *Penicillium* species, particularly *Penicilliumexpansum*, are responsible for blue mold rot, primarily affecting apples, pears, and citrus fruits. The fungal spores can survive in storage environments and contaminate fruits through small injuries or lenticels [6]. These pathogens produce mycotoxins, such as patulin, which pose significant health risks to consumers, making fungal pathogens a critical concern in the post-harvest phase.

2. Bacterial Pathogens (e.g., *Erwinia spp.*, *Pseudomonas spp.*)

Bacterial pathogens, although less prevalent than fungi, are also major contributors to post-harvest diseases. *Erwinia spp.*, responsible for soft rot in vegetables like potatoes, carrots, and onions, cause rapid tissue degradation by producing pectolytic enzymes that break down cell walls, leading to a watery, foul-smelling rot .*Pseudomonas spp.*, particularly *Pseudomonas syringae*, are associated with bacterial speck and soft rot in fruits like tomatoes and peppers. These bacteria often enter through wounds and thrive in moist environments, leading to significant spoilage during storage and transportation. Unlike fungal pathogens, bacterial infections spread more rapidly in high-humidity conditions, making their management in storage facilities a critical challenge for maintaining post-harvest quality.

3. Viral Pathogens Affecting Post-Harvest Quality

While viral pathogens are less frequently associated with post-harvest diseases compared to fungi and bacteria, they still play a role in reducing the quality of stored fruits and vegetables [7]. Viruses such as the Tomato spotted wilt virus (TSWV) and Cucumber mosaic virus (CMV) can cause symptoms like discoloration, mottling, and malformation in fruits, leading to a decline in market value. Viruses are typically introduced during the growing period and persist in the harvested produce, with symptoms often becoming more pronounced during storage. The lack of direct chemical control methods for viral pathogens further complicates the management of viral diseases in post-harvest settings, necessitating preventative measures during the cultivation phase.

B. Economic Impact of Post-Harvest Diseases

Post-harvest diseases significantly impact the global economy, contributing to substantial losses in the fruit and vegetable industry. According to the Food and Agriculture Organization (FAO), approximately 20-40% of fruits and vegetables are lost annually due to post-harvest diseases, depending on the region and crop type [8]. These losses translate into billions of dollars in wasted food, reduced income for farmers, and increased costs for consumers. The economic burden is particularly severe in developing countries, where inadequate storage facilities and poor handling practices exacerbate the incidence of post-harvest spoilage. In addition to the direct losses from spoilage, post-harvest diseases also reduce the marketability of produce by affecting its visual appeal, nutritional quality, and safety, further diminishing its commercial value. Moreover, the costs associated with managing post-harvest diseases, including the use of fungicides, bactericides, and other control measures, add to the financial strain on producers and distributors. As global demand for fresh produce continues to rise, the need to address post-harvest diseases becomes increasingly urgent, both for economic sustainability and for ensuring food security [9].

C. Factors Contributing to Post-Harvest Disease Susceptibility

Several factors contribute to the susceptibility of fruits and vegetables to post-harvest diseases, many of which are influenced by environmental conditions, storage practices, and the physiological state of the produce. These factors collectively determine the extent to which pathogens can invade and cause spoilage during the post-harvest phase.

1. Environmental Conditions (Humidity, Temperature)

Environmental conditions play a pivotal role in the development and spread of post-harvest diseases. High humidity levels in storage environments create favorable conditions for fungal and bacterial pathogens, allowing them to proliferate rapidly on the surface of fruits and vegetables. Temperature is another critical factor; warm temperatures accelerate the metabolic activity of pathogens, leading to faster disease progression, while excessively low temperatures can cause chilling injuries in sensitive fruits like bananas and tomatoes, making them more prone to infection. Proper control of temperature and humidity in storage facilities is essential to reducing the incidence of post-harvest diseases and maintaining the quality of produce over time [10].

2. Storage and Handling Practices

The way fruits and vegetables are stored and handled after harvest significantly affects their susceptibility to post-harvest diseases. Poor handling practices, such as rough picking, bruising, and exposure to contaminated surfaces, provide entry points for pathogens to invade the produce. Improper storage conditions, including inadequate ventilation and overcrowding, further increase the risk of disease by creating environments that are conducive to pathogen growth. Moreover, the duration of storage also plays a role; extended storage periods provide more time for pathogens to establish and cause decay, particularly if the produce is not stored under optimal conditions. Advances in post-harvest handling technologies, including modified atmosphere packaging (MAP) and the use of antimicrobial coatings, have shown promise in reducing pathogen invasion and extending the shelf life of fresh produce [11].

3. Physiological State of the Fruit or Vegetable

The physiological condition of the fruit or vegetable at harvest has a direct influence on its susceptibility to post-harvest diseases. Overripe or damaged produce is more vulnerable to pathogen attack due to weakened cell structures and increased sugar content, which provide a more favorable environment for microbial growth.

Table 1. Post-harvest diseases in fruits and vegetables source: [7,8,11]

Crop	Disease	Causal Organism	Symptoms	Control Measures
Apples	Blue Mold	*Penicillium expansum*	Soft, watery lesions on fruit; blue-green spore masses	Proper storage temperature, fungicide treatments, sanitation
Bananas	Anthracnose	*Colletotrichum musae*	Black, sunken lesions on peel; fruit rot	Hot water treatment, fungicides, and avoiding mechanical injury
Tomatoes	Gray Mold	*Botrytis cinerea*	Grayish fungal growth on fruit surface; soft rot	Controlled atmosphere storage, fungicide sprays, ventilation
Citrus Fruits	Green Mold	*Penicillium digitatum*	Green spore masses on fruit; soft rot	Post-harvest fungicide dips, storage hygiene
Grapes	Black Rot	*Guignardia bidwellii*	Black, shriveled berries, often with concentric rings	Pruning infected parts, sulfur fungicide sprays
Strawberries	Rhizopus Rot	*Rhizopus stolonifer*	Soft, watery fruit with cottony fungal growth	Cold storage, fungicide application, careful handling
Peppers	Bacterial Soft Rot	*Erwinia carotovora*	Soft, water-soaked lesions leading to fruit collapse	Sanitation, proper handling, post-harvest treatments
Carrots	Sclerotinia Rot	*Sclerotinia sclerotiorum*	Watery, soft rot with white fungal growth	Fungicide sprays, proper storage conditions
Potatoes	Dry Rot	*Fusarium spp.*	Dry, sunken lesions with wrinkled skin; internal discoloration	Use of disease-free tubers, proper curing, fungicide treatment
Onions	Neck Rot	*Botrytis allii*	Soft rot starting from the neck; fungal growth on scales	Proper curing, fungicide sprays, avoidance of moisture during storage

3. MECHANISMS OF INDUCED RESISTANCE

A. History

Induced resistance (IR) refers to a plant’s enhanced ability to defend itself against pathogen attacks after being exposed to specific environmental or chemical stimuli (Table 2) [12]. The concept of induced resistance dates back to the early 20th century when Chester (1933) proposed the idea of "acquired immunity" in plants, similar to that observed in animals. Since then, the study of plant defense mechanisms has evolved significantly, with researchers identifying various pathways through which plants can activate defense responses against pathogens. Induced resistance is now recognized as a broad-spectrum and durable form of resistance that can be triggered by biotic agents such as pathogens, beneficial microorganisms, or even abiotic factors like chemicals and environmental stressors. Over the past decades, considerable progress has been made in understanding the underlying mechanisms of induced resistance, particularly through the study of signaling molecules, gene expression, and the interplay between different resistance pathways. As a sustainable alternative to chemical pesticides, induced resistance has attracted increasing interest in the context of integrated pest management and post-harvest disease control [13].

B. Types of Induced Resistance in Plants

Induced resistance in plants can be categorized into several distinct types, each associated with specific signaling pathways and molecular responses. The two most well-characterized forms of induced resistance are Systemic Acquired Resistance (SAR) and Induced Systemic Resistance (ISR), both of which are activated by different stimuli and regulated by distinct signaling molecules. Additionally, the concept of priming, in which plants are conditioned to respond more rapidly and robustly to pathogen attacks, has gained recognition as an important aspect of induced resistance [14].

1. Systemic Acquired Resistance (SAR)

Systemic Acquired Resistance (SAR) is a form of induced resistance that occurs after a plant is exposed to a localized pathogen attack or other types of damage, leading to the activation of defense responses throughout the entire plant. SAR is typically associated with the accumulation of salicylic acid (SA) and the production of pathogenesis-related (PR) proteins, which play a crucial role in enhancing the plant's immunity against a wide range of pathogens. Once SAR is triggered, the plant develops a heightened state of defense, enabling it to resist subsequent infections by unrelated pathogens. The signaling molecule salicylic acid is a key mediator of SAR, and its systemic movement through the plant triggers defense gene expression in distal tissues. The molecular markers of SAR include the expression of PR genes, which encode enzymes such as chitinases and glucanases that degrade the cell walls of invading pathogens [15]. Studies have demonstrated that SAR provides long-lasting protection and has been successfully utilized to manage various diseases in agricultural crops.

2. Induced Systemic Resistance (ISR)

Induced Systemic Resistance (ISR) is another form of induced resistance, primarily activated by beneficial microorganisms such as plant growth-promoting rhizobacteria (PGPR) and mycorrhizal fungi. Unlike SAR, which relies on salicylic acid, ISR is regulated by jasmonic acid (JA) and ethylene (ET) signaling pathways. The beneficial microorganisms colonize plant roots and trigger systemic defense responses, enabling the plant to resist a broad range of pathogens, including bacteria, fungi, and viruses. ISR does not involve the direct accumulation of PR proteins; instead, it primes the plant’s existing defense mechanisms to respond more effectively to pathogen attacks. This primed state enables the plant to rapidly activate defense responses, such as the production of antimicrobial compounds and reinforcement of cell walls, upon pathogen invasion [16]. ISR has been extensively studied in both model plants and agricultural crops, with numerous examples of its effectiveness in enhancing resistance to post-harvest pathogens.

3. Priming of Plant Defenses

Priming is a phenomenon in which plants, after being exposed to certain stimuli, develop a heightened ability to respond to subsequent pathogen attacks. While SAR and ISR involve the activation of specific defense pathways, priming refers to the plant’s ability to remain in a latent defensive state until it is challenged by a pathogen. Primed plants respond faster and more strongly to pathogen attacks by activating defense-related genes, producing antimicrobial compounds, and strengthening physical barriers. The molecular basis of priming involves epigenetic modifications, such as changes in chromatin structure, that allow defense genes to be rapidly activated upon pathogen challenge. Priming can be induced by biotic factors, such as pathogen infection, or abiotic factors, such as chemical treatments or environmental stress [17]. Priming is considered a highly efficient form of induced resistance, as it allows plants to conserve energy by not constantly activating defense mechanisms, while still being able to mount a rapid and effective response when needed.

C. Molecular Basis of Induced Resistance

The molecular mechanisms underlying induced resistance involve a complex network of signaling molecules, defense-related proteins, and cross-talk between different signaling pathways. These molecular components work together to activate and coordinate the plant’s defense responses, ensuring a broad-spectrum and long-lasting resistance to pathogens.

1. Role of Signaling Molecules (Salicylic Acid, Jasmonic Acid, Ethylene)

Salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) are the three main signaling molecules that regulate induced resistance in plants [18]. These molecules act as key mediators of plant defense responses, activating specific pathways in response to pathogen attacks. Salicylic acid is primarily associated with SAR and plays a crucial role in activating defense genes and PR proteins that provide systemic resistance against biotrophicpathogens .Jasmonic acid and ethylene, on the other hand, are involved in the regulation of ISR and are crucial for defending against necrotrophic pathogens and insect herbivores. The JA and ET pathways work synergistically to activate defense mechanisms, such as the production of antimicrobial compounds and the reinforcement of cell walls. The dynamic interplay between these signaling molecules allows plants to fine-tune their defense responses based on the type of pathogen they encounter [19].

2. Gene Expression and Defense-Related Proteins

Induced resistance involves the activation of a wide range of defense-related genes, many of which encode proteins involved in pathogen recognition, signal transduction, and the production of antimicrobial compounds. In the case of SAR, the expression of PR genes is a hallmark of the defense response. These PR proteins, including chitinases, glucanases, and peroxidases, degrade the cell walls of invading pathogens and inhibit their growth. In addition to PR proteins, plants produce a variety of secondary metabolites, such as phytoalexins, which have antimicrobial properties. In ISR, defense-related proteins such as protease inhibitors and polyphenol oxidases are upregulated in response to JA and ET signaling, contributing to the plant's ability to resist necrotrophic pathogens. The coordinated expression of these defense-related genes ensures a comprehensive defense response that protects the plant from a wide range of pathogens [20].

3. Cross-Talk Between Signaling Pathways

One of the most intriguing aspects of induced resistance is the cross-talk between different signaling pathways, which allows plants to integrate multiple defense signals and optimize their responses to different types of pathogens. The interaction between the SA, JA, and ET pathways is a key example of this cross-talk. While SAR is primarily regulated by SA, there is evidence that JA and ET can influence SAR signaling, and vice versa. This cross-talk enables plants to tailor their defense responses based on the specific nature of the pathogen attack [21]. For example, biotrophic pathogens, which feed on living plant tissue, tend to activate SA-dependent defenses, while necrotrophic pathogens, which kill plant cells, activate JA- and ET-dependent defenses. The ability of plants to integrate signals from different pathways ensures that they can mount an effective and appropriate defense response, regardless of the type of pathogen they encounter.

4. INDUCED RESISTANCE IN FRUITS AND VEGETABLES

A. Natural Plant Defense Mechanisms Against Post-Harvest Pathogens

Fruits and vegetables possess inherent defense mechanisms that help protect them against post-harvest pathogens. These natural defense systems are activated in response to pathogen attacks and are composed of both physical and biochemical barriers. Physical defenses include the structural integrity of the plant's epidermal layers, cell walls, and waxy cuticles, which act as a first line of defense to prevent pathogen entry (Table 2) [22]. Once the pathogen breaches these barriers, plants deploy biochemical defenses such as the production of reactive oxygen species (ROS), phytoalexins, and defense-related enzymes like chitinases, glucanases, and peroxidases. These biochemical responses disrupt the pathogen’s cellular processes and degrade its cell walls, limiting its ability to establish infection. Fruits and vegetables may contain secondary metabolites, including phenolics, tannins, and flavonoids, which exhibit antimicrobial properties and inhibit the growth of pathogens. In some cases, plants synthesize specific proteins that inhibit pathogen activity, such as pathogenesis-related (PR) proteins that degrade pathogen cell walls or prevent fungal spore germination. Natural defense mechanisms are crucial for slowing the progression of post-harvest diseases and are often enhanced through the process of induced resistance. These mechanisms can weaken after harvest due to physiological changes, making external intervention through induced resistance strategies essential for effective post-harvest disease control [23].

B. Efficacy of Induced Resistance in Fruit and Vegetable Crops

Induced resistance has shown considerable efficacy in mitigating post-harvest diseases in both fruits and vegetables. By enhancing the natural defense mechanisms of these crops, induced resistance provides a sustainable and environmentally friendly alternative to traditional chemical pesticides. Research has demonstrated that various forms of induced resistance, including systemic acquired resistance (SAR), induced systemic resistance (ISR), and priming, can significantly reduce the incidence of post-harvest spoilage caused by fungal, bacterial, and viral pathogens. The efficacy of induced resistance in fruit and vegetable crops depends on factors such as the type of inducer used, the plant species, and the specific pathogen targeted [24].

1. Case Studies on Fruits (e.g., Apples, Tomatoes, Citrus)

Numerous studies have demonstrated the successful application of induced resistance in fruit crops. For instance, in apples, SAR induced by acibenzolar-S-methyl (ASM), a chemical analogue of salicylic acid, has been shown to reduce the incidence of blue mold caused by *Penicilliumexpansum*. The treatment led to increased expression of PR proteins and phenolic compounds in apple tissues, enhancing resistance against fungal infection. Similarly, ISR induced by *Pseudomonas fluorescens* has proven effective in controlling gray mold (*Botrytis cinerea*) in tomatoes. The bacterium triggers a defense response through the jasmonic acid and ethylene pathways, leading to the production of antimicrobial compounds and strengthening of cell walls. In citrus fruits, treatments with methyl jasmonate have been shown to enhance resistance against green mold caused by *Penicilliumdigitatum*, reducing spoilage during storage [25]. These case studies highlight the versatility of induced resistance in protecting fruit crops from various post-harvest pathogens.

2. Case Studies on Vegetables (e.g., Potatoes, Peppers)

In vegetables, induced resistance has also proven effective in reducing post-harvest diseases. Potatoes treated with harpin proteins, a group of bacterial proteins known to elicit defense responses in plants, showed increased resistance to soft rot caused by *Pectobacteriumcarotovorum*. The treatment enhanced the expression of defense-related genes and the production of antimicrobial enzymes, significantly reducing the severity of the disease during storage. In peppers, induced resistance through the application of beneficial rhizobacteria such as *Bacillus subtilis* has been shown to control post-harvest pathogens like *Colletotrichum* species, which cause anthracnose. The bacteria triggered ISR in the pepper plants, leading to the accumulation of defense-related compounds and reduced pathogen colonization [26]. These findings indicate that induced resistance can be successfully applied to a wide range of vegetable crops to protect against post-harvest diseases.

C. Methods of Inducing Resistance in Post-Harvest Products

Various methods are available to induce resistance in post-harvest products, ranging from biological and chemical inducers to physical treatments. These methods aim to enhance the plant's innate immune responses or prime the plant for a more rapid and robust defense against pathogen attacks during the post-harvest phase.

1. Biological Inducers (Beneficial Microorganisms, Biocontrol Agents)

Biological inducers, including beneficial microorganisms such as plant growth-promoting rhizobacteria (PGPR) and biocontrol agents, play a critical role in inducing resistance in post-harvest crops [27]. These microorganisms interact with plant roots or surfaces, triggering systemic defense responses without causing harm to the plant. For instance, *Bacillus subtilis* and *Pseudomonas fluorescens* have been widely used as biological inducers to control post-harvest pathogens. These beneficial bacteria colonize the root or fruit surfaces and activate ISR, leading to the accumulation of defense-related compounds such as phytoalexins and phenolics, which inhibit pathogen growth. Biocontrol agents like *Trichoderma* species have been used to induce resistance in various crops by competing with pathogens for space and resources, as well as by activating the plant's defense mechanisms through signaling pathways [28].

2. Chemical Inducers (Plant Hormones, Elicitors)

Chemical inducers such as plant hormones and synthetic elicitors are also effective in triggering induced resistance in post-harvest crops. Salicylic acid, jasmonic acid, and ethylene are key plant hormones that regulate defense responses in plants. Exogenous application of these hormones or their analogs can activate SAR and ISR, leading to enhanced resistance against post-harvest pathogens. For example, methyl jasmonate has been used to induce resistance in citrus fruits against green mold, while salicylic acid analogs have been applied to apples to control blue mold caused by *Penicilliumexpansum* . Elicitors such as chitosan, a natural polysaccharide derived from chitin, have also been used to induce resistance in post-harvest products [29]. Chitosan treatments have been shown to activate defense-related enzymes and strengthen cell walls in fruits and vegetables, reducing the severity of post-harvest diseases.

3. Physical Methods (Heat Treatment, UV Light)

Physical methods such as heat treatment and ultraviolet (UV) light exposure are also employed to induce resistance in post-harvest products. Heat treatment, including hot water dips or vapor heat, has been shown to enhance resistance to post-harvest pathogens by inducing the production of heat shock proteins and other defense-related compounds in fruits and vegetables. For instance, heat treatment has been used to control anthracnose in mangoes and reduce decay in tomatoes during storage.

Table 2. Induced resistance in fruits and vegetables

Fruit/ Vegetable	Type of Induced Resistance	Inducing Agent	Mode of Action	Examples of Resistance Outcome
Tomato	Systemic Acquired Resistance (SAR)	*Salicylic Acid (SA)*, Biocontrol agents (*Bacillus spp.*)	Activation of defense-related genes, production of pathogenesis-related proteins (PR)	Enhanced resistance to *Botrytis cinerea*, *Phytophthora infestans*
Cucumber	Induced Systemic Resistance (ISR)	Plant Growth-Promoting Rhizobacteria (PGPR), *Pseudomonas spp.*	Induces non-specific systemic resistance through jasmonic acid (JA) and ethylene pathways	Reduced severity of *Pythium aphanidermatum*, *Sclerotinia sclerotiorum*
Apple	Systemic Acquired Resistance (SAR)	Chitosan, Beta-aminobutyric acid (BABA)	Enhances natural plant defenses by increasing phenolic content and lignification	Resistance to blue mold (*Penicillium expansum*) and fire blight (*Erwinia amylovora*)
Pepper	Induced Systemic Resistance (ISR)	*Trichoderma harzianum*, Mycorrhizal fungi	Enhances plant resistance via increased secondary metabolites and antioxidant activity	Resistance to *Phytophthora capsici*, *Rhizoctonia solani*
Grapes	Systemic Acquired Resistance (SAR)	*Bacillus subtilis*, Oligosaccharides	Induces oxidative burst, accumulation of phytoalexins	Increased resistance to gray mold (*Botrytis cinerea*)
Banana	Induced Systemic Resistance (ISR)	*Pseudomonas fluorescens*, Seaweed extract	Boosts root defense mechanisms, induces phytohormone pathways	Reduced incidence of fusarium wilt (*Fusarium oxysporum*)
Strawberry	Systemic Acquired Resistance (SAR)	Methyl jasmonate, Chitosan	Activates defense enzymes such as peroxidase and phenylalanine ammonia-lyase (PAL)	Reduced gray mold infection (*Botrytis cinerea*)
Carrot	Induced Systemic Resistance (ISR)	*Rhizobacteria*, Mycorrhizal fungi	Activates jasmonic acid and ethylene signaling pathways	Increased resistance to root-knot nematode (*Meloidogyne spp.*)
Potato	Systemic Acquired Resistance (SAR)	Beta-aminobutyric acid (BABA), Acibenzolar-S-Methyl (ASM)	Stimulates defense mechanisms including reactive oxygen species (ROS) production	Resistance to late blight (*Phytophthora infestans*)

UV light exposure is another method used to induce resistance by triggering the production of antimicrobial compounds and strengthening the plant's physical barriers [30]. UV-C light, in particular, has been shown to reduce the incidence of post-harvest diseases such as gray mold in strawberries and green mold in citrus fruits by inducing the accumulation of phenolic compounds and activating defense-related enzymes.

5. BIOCHEMICAL AND PHYSIOLOGICAL CHANGES DURING INDUCED RESISTANCE

D. Activation of Defense-Related Enzymes (Chitinases, Glucanases, Peroxidases)

Induced resistance in plants triggers the activation of several key defense-related enzymes, including chitinases, glucanases, and peroxidases, which play crucial roles in enhancing the plant's ability to resist pathogen invasion. Chitinases are enzymes that degrade chitin, a major structural component of fungal cell walls, thereby inhibiting the growth and spread of fungal pathogens. Studies have shown that plants treated with inducers of systemic acquired resistance (SAR) or induced systemic resistance (ISR) exhibit increased activity of chitinases, which significantly reduces fungal infection .Glucanases are another group of hydrolytic enzymes that break down glucans, which are polysaccharides found in the cell walls of fungi [31]. These enzymes work in concert with chitinases to degrade pathogen cell walls, making it difficult for fungi to colonize plant tissues. Peroxidases, on the other hand, are involved in the generation of reactive oxygen species (ROS) and the cross-linking of cell wall components, which strengthens plant cell walls and limits pathogen penetration. The activation of these defense-related enzymes is a hallmark of induced resistance, as they provide a biochemical barrier that hinders pathogen entry and establishment in plant tissues [32].

B. Accumulation of Secondary Metabolites (Phytoalexins, Phenolics)

Induced resistance is also associated with the accumulation of secondary metabolites such as phytoalexins and phenolics, which are critical for inhibiting pathogen growth and spread. Phytoalexins are low-molecular-weight antimicrobial compounds that are synthesized by plants in response to pathogen attack. These compounds disrupt the cellular processes of pathogens, leading to their death or reduced virulence. For example, in grapevines, the accumulation of the phytoalexin resveratrol has been shown to inhibit the growth of *Botrytis cinerea*, a fungal pathogen responsible for gray mold in many fruit crops. In soybeans, the phytoalexinglyceollin plays a key role in defending against fungal pathogens such as *Phytophthorasojae*. Phenolic compounds, including flavonoids and tannins, are another class of secondary metabolites that contribute to plant defense. These compounds have antimicrobial properties and can inhibit the enzymes produced by pathogens to degrade plant cell walls. In addition, phenolics play a role in lignification, a process that reinforces cell walls and limits pathogen entry [33]. The accumulation of secondary metabolites is a key biochemical response in induced resistance, as it provides plants with potent chemical defenses that deter pathogen colonization.

C. Strengthening of Cell Walls to Prevent Pathogen Invasion

One of the primary physiological changes that occurs during induced resistance is the strengthening of plant cell walls, which serves as a physical barrier against pathogen invasion. This is achieved through the deposition of lignin, suberin, and callose in the cell walls, which increases their rigidity and impermeability. Lignin is a complex polymer that reinforces cell walls by cross-linking with other cell wall components, making it more difficult for pathogens to penetrate. Suberin and callose are other components that are deposited in response to pathogen attack; they form a protective layer that seals off infected or damaged tissues, thereby preventing the spread of pathogens. The process of cell wall fortification is often mediated by enzymes such as peroxidases, which catalyze the cross-linking of cell wall polymers in the presence of reactive oxygen species (ROS) [34]. This structural modification of the cell wall is a critical aspect of induced resistance, as it provides a robust defense against a wide range of pathogens, including fungi, bacteria, and viruses.

D. Role of Reactive Oxygen Species (ROS) in Defense

Reactive oxygen species (ROS), including superoxide anions, hydrogen peroxide, and hydroxyl radicals, play a pivotal role in plant defense mechanisms during induced resistance. ROS are produced rapidly in response to pathogen recognition and serve multiple functions in plant defense. First, ROS act as signaling molecules that activate downstream defense responses, including the expression of defense-related genes and the production of antimicrobial compounds. Second, ROS are directly toxic to pathogens, causing oxidative damage to their cellular components such as lipids, proteins, and nucleic acids. This oxidative burst helps to limit pathogen proliferation and spread [35]. Third, ROS are involved in the strengthening of plant cell walls by catalyzing the cross-linking of cell wall polymers, which enhances the physical barrier against pathogen invasion. The production of ROS must be tightly regulated, as excessive ROS can cause damage to plant cells. Plants have evolved antioxidant systems, including enzymes such as superoxide dismutase (SOD) and catalase, to modulate ROS levels and prevent oxidative stress. The controlled production of ROS is therefore a key component of the plant’s induced resistance strategy, as it contributes to both biochemical and physical defenses.

6. APPLICATION OF INDUCED RESISTANCE IN POST-HARVEST DISEASE MANAGEMENT

A. Practical Applications in Commercial Agriculture

The practical application of induced resistance in commercial agriculture offers a sustainable and environmentally friendly approach to managing post-harvest diseases in fruits and vegetables [36]. Unlike traditional chemical fungicides, which can lead to the development of resistant pathogen strains and pose environmental risks, induced resistance enhances the plant’s innate immune system, reducing the need for external chemical inputs. This method has been successfully implemented in the management of post-harvest diseases such as gray mold, blue mold, and soft rot, which affect a wide range of crops, including apples, grapes, tomatoes, and potatoes . The use of natural or synthetic inducers, such as salicylic acid analogs, jasmonic acid, beneficial microorganisms, and plant growth-promoting rhizobacteria (PGPR), has been shown to effectively reduce disease incidence in commercial storage and transportation systems. These treatments are often applied as pre-harvest foliar sprays or post-harvest dips, providing long-lasting protection against pathogens during storage and marketing [37].

B. Integration of Induced Resistance with Other Disease Management Strategies

To maximize the effectiveness of induced resistance in post-harvest disease management, it is often integrated with other disease control strategies. This integrated approach helps to provide a more comprehensive and sustainable solution to post-harvest diseases.

1. Use of Biological Control Agents

The integration of induced resistance with biological control agents, such as antagonistic fungi and bacteria, has proven effective in managing post-harvest diseases. For instance, the use of *Trichoderma* species as biocontrol agents has been shown to induce systemic resistance in fruits and vegetables while also directly inhibiting the growth of post-harvest pathogens through competition and antibiosis [38]. Similarly, the combination of ISR-inducing bacteria, such as *Pseudomonas fluorescens*, with biocontrol agents like *Candida sake*, has been shown to enhance resistance against gray mold in strawberries during storage.

2. Combination with Conventional Fungicides

Induced resistance can also be combined with conventional fungicides to achieve more effective disease control while reducing the overall fungicide load. This combination strategy allows for lower doses of fungicides to be used, thereby minimizing the risk of pathogen resistance development and reducing environmental impact. Studies have demonstrated that induced resistance treatments can enhance the efficacy of fungicides by priming the plant’s defense mechanisms, making pathogens more susceptible to chemical treatments. For example, the combination of SAR-inducing agents with fungicides has been shown to reduce blue mold incidence in apples with lower fungicide dosages than conventional treatments [39].

3. Role of Post-Harvest Handling and Storage Practices

The success of induced resistance in managing post-harvest diseases is also dependent on proper post-harvest handling and storage practices. Maintaining optimal storage conditions, such as appropriate temperature, humidity, and ventilation, can enhance the effectiveness of induced resistance by minimizing stress on the fruit or vegetable and reducing the likelihood of pathogen infection. Practices such as careful handling to avoid bruising or mechanical damage can prevent the introduction of entry points for pathogens, thereby complementing the protective effects of induced resistance [40].

C. Case Studies on Successful Implementation of Induced Resistance

Several case studies have demonstrated the successful implementation of induced resistance in commercial agriculture. In apples, the use of acibenzolar-S-methyl (ASM), a synthetic SAR inducer, has been shown to significantly reduce the incidence of blue mold caused by *Penicilliumexpansum* during storage. This treatment enhanced the production of defense-related enzymes and phenolic compounds in apple tissues, leading to long-lasting protection against fungal infection. In grapes, the application of ISR-inducing bacteria, such as *Bacillus subtilis*, has been effective in reducing gray mold incidence during post-harvest storage by triggering systemic defense responses in the fruit. Another successful case study involves the use of methyl jasmonate in citrus fruits to induce resistance against green mold (*Penicilliumdigitatum*), resulting in reduced spoilage and extended shelf life during storage [41]. These case studies highlight the potential of induced resistance to be effectively integrated into post-harvest disease management programs in commercial agriculture, providing sustainable solutions to reduce crop losses and improve food security.

7. CHALLENGES AND LIMITATIONS OF INDUCED RESISTANCE

A. Variability in Effectiveness among Different Crops and Pathogens

Induced resistance (IR) has shown significant potential in managing post-harvest diseases; however, its effectiveness can vary widely across different crops and pathogen types. This variability is primarily due to differences in the genetic makeup of crops and the diversity of pathogens they encounter. For instance, while SAR (Systemic Acquired Resistance) may be highly effective in apples against blue mold caused by *Penicilliumexpansum*, the same treatment might be less effective in citrus fruits against *Penicilliumdigitatum*, the causal agent of green mold. ISR (Induced Systemic Resistance), which is typically triggered by rhizobacteria, may provide robust defense against *Botrytis cinerea* in tomatoes, but its efficacy might be inconsistent in other crops like grapes, where pathogen pressure and environmental conditions differ [42]. The inconsistency in IR's effectiveness stems from the fact that different crops have varying defense capabilities, and different pathogens may employ distinct mechanisms of attack that evade or suppress the plant's induced resistance responses. Moreover, the same pathogen species may exhibit different virulence factors across various host crops, further complicating the effectiveness of IR treatments.

B. Environmental Factors Affecting Induced Resistance

Environmental conditions play a critical role in the success of induced resistance, as factors such as temperature, humidity, and light can significantly influence the plant's ability to mount an effective defense response. For example, high humidity levels can promote the proliferation of fungal pathogens, overwhelming the plant's induced defenses [43]. Conversely, low humidity may inhibit the production of certain defense-related compounds, reducing the efficacy of IR. Temperature fluctuations can also impact IR; extreme temperatures, either too high or too low, can suppress the signaling pathways involved in SAR and ISR, leading to reduced pathogen resistance. Studies have shown that ISR, which relies on jasmonic acid and ethylene signaling, is more effective under certain environmental conditions, such as moderate temperatures and adequate soil moisture, while unfavorable conditions can limit its effectiveness. Abiotic stressors like drought or nutrient deficiency can weaken the plant's defense responses, making it more susceptible to pathogen attack even after induction of resistance. Therefore, the success of induced resistance strategies is often dependent on optimizing environmental conditions to support the plant's immune system [44].

C. Potential Trade-offs (e.g., Reduced Yield, Fruit Quality Issues)

While induced resistance can enhance a plant's defense mechanisms, there are potential trade-offs that must be considered, particularly in terms of yield and fruit quality. The activation of defense responses requires energy and resources, which may be diverted from growth and reproductive processes, leading to reduced yield or lower quality fruits. For instance, studies have shown that the overexpression of defense-related genes, particularly those involved in SAR, can result in stunted growth or delayed ripening in some crops. The accumulation of defense compounds such as phenolics and phytoalexins, while beneficial for pathogen resistance, can sometimes negatively affect the sensory qualities of fruits, including taste, texture, and appearance [45]. For example, increased levels of phenolic compounds in fruits like strawberries or apples may lead to undesirable browning or bitterness, which can reduce consumer acceptance. These trade-offs highlight the need for a balanced approach in implementing induced resistance, ensuring that enhanced disease resistance does not come at the expense of crop yield or marketability.

D. Need for Further Research and Development

Despite the promising results of induced resistance in controlling post-harvest diseases, there is still a considerable need for further research and development to fully harness its potential. One of the key areas that requires more investigation is the optimization of IR treatments for different crops and pathogen types [46]. This includes identifying the most effective inducers, understanding the molecular mechanisms behind plant-pathogen interactions, and determining how IR can be combined with other disease management strategies for maximum efficacy. Additionally, more research is needed to address the variability in IR effectiveness across different environmental conditions and to develop formulations that are more stable and reliable under diverse growing conditions.

8. FUTURE

A. Advances in Genetic Engineering for Enhanced Resistance

Genetic engineering presents exciting prospects for enhancing induced resistance in crops. With the advent of CRISPR-Cas9 and other gene-editing technologies, it is now possible to precisely manipulate the genes involved in plant defense pathways, potentially leading to crops with enhanced resistance to a wide range of pathogens. For instance, by overexpressing key genes in the salicylic acid (SA) or jasmonic acid (JA) signaling pathways, researchers can enhance SAR or ISR responses in plants, making them more resistant to post-harvest diseases [47]. Additionally, genetic engineering can be used to introduce resistance genes from other species or to silence genes that pathogens use to suppress the plant's immune system. These advances have already shown promise in model plants and are gradually being applied to commercial crops. However, the regulatory and public acceptance of genetically modified organisms (GMOs) remains a challenge, particularly in markets with stringent regulations on biotechnology.

B. Development of New Inducers and Formulations

Another exciting area of innovation is the development of new inducers and formulations to trigger induced resistance more effectively and reliably [48]. While traditional inducers like salicylic acid and jasmonic acid have been widely used, researchers are now exploring novel elicitors, including plant-derived peptides, microbial metabolites, and synthetic compounds, that can more precisely activate the desired defense pathways without the trade-offs associated with traditional inducers. In addition, advancements in formulation technology, such as controlled-release systems and nanotechnology-based delivery methods, are being developed to improve the stability and efficacy of IR treatments. For example, nanomaterials can be used to encapsulate inducers and ensure their slow release over time, providing sustained protection against pathogens during storage and transportation. These innovations hold the potential to make induced resistance more practical and accessible for commercial agriculture, particularly in the context of post-harvest disease management [49].

C. Potential for Integrating Precision Agriculture Technologies

The integration of precision agriculture technologies with induced resistance offers a promising avenue for improving the management of post-harvest diseases. Precision agriculture involves the use of advanced technologies such as remote sensing, drones, and data analytics to monitor crop health, environmental conditions, and pathogen pressure in real-time. By combining these technologies with induced resistance strategies, farmers can more accurately time the application of inducers, optimize environmental conditions to support plant defense responses, and target specific areas of the crop that are most vulnerable to pathogen attack. For instance, drones equipped with hyperspectral sensors can detect early signs of disease or stress in crops, allowing for the precise application of IR treatments before the pathogen spreads. This integration of technology not only improves the efficiency of induced resistance but also reduces the overall use of chemical inputs, making it a more sustainable approach to disease management [50].

D. Long-Term Sustainability of Induced Resistance in Agriculture

The long-term sustainability of induced resistance in agriculture will depend on several factors, including its effectiveness across different crops and pathogens, its integration with other disease management strategies, and its ability to adapt to changing environmental conditions. One of the key advantages of induced resistance is its potential to reduce the reliance on chemical fungicides, which are often associated with negative environmental impacts and the development of resistant pathogen strains. By enhancing the plant's natural defenses, IR provides a more sustainable approach to managing diseases without the need for continuous chemical applications. However, for IR to remain sustainable in the long term, it must be implemented as part of an integrated pest management (IPM) strategy that includes biological control agents, cultural practices, and environmental monitoring [51]. Additionally, ongoing research and innovation will be crucial to overcoming the challenges and limitations of IR, ensuring that it can continue to provide effective protection against post-harvest diseases in a wide range of crops and farming systems.

9. CONCLUSION

Induced resistance represents a promising and sustainable approach to managing post-harvest diseases in fruits and vegetables. By enhancing the plant's natural defense mechanisms, induced resistance offers broad-spectrum protection against a wide range of pathogens without the need for excessive chemical inputs. However, its effectiveness can vary depending on crop type, pathogen species, and environmental conditions, necessitating further research and optimization. While challenges such as potential trade-offs in yield and fruit quality remain, advancements in genetic engineering, novel inducers, and precision agriculture technologies offer exciting prospects for improving the efficacy and reliability of induced resistance. Integrating induced resistance with other disease management strategies, including biological control and optimized storage practices, will be essential for its long-term sustainability and broader application in commercial agriculture.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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