Review Article

Postharvest Pathogens in Strawberry (*Fragaria x ananassa*): Potential of Plasma-Activated Water and Micro-Nano Bubbles for Control – A Review

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Abstract
Pathogen contamination of strawberries is a significant concern, as it leads to yield losses and a decrease in consumer acceptance. The quality and safety of strawberries are particularly vulnerable to fungal and bacterial pathogens, which can affect fruits during cultivation, transportation, and storage. Among the primary fungal pathogens responsible for their quality deterioration are *Botrytis cinerea*, *Rhizopus* spp., *Colletotrichum* spp., and *Penicillium* spp. In addition, strawberries are also vulnerable to bacterial pathogens, including *Salmonella* spp., *Escherichia coli*, *Listeria monocytogenes*, and *Staphylococcus* spp. Over the past few decades, researchers have developed several control methods to improve their quality and ensure safe consumption. These include chemical, physical, and biological controls. However, the lack of effective pathogen inactivation during postharvest remains a challenge. Plasma-activated water (PAW), which is rich in reactive oxygen and nitrogen species (RONS), has demonstrated pathogen inactivation abilities. Similarly, the properties of micro-nano bubbles (MNBs), such as a large specific surface area, a long lifetime in aqueous solutions, oxidizing ability, and reduction of surface tension, have been studied for disinfection applications. Therefore, this article provides a comprehensive overview of the morphological and pathogenic variability of the common fungal and bacterial pathogens in strawberries. Furthermore, it highlights the pathogen-inactivating ability of PAW and MNBs as a potential postharvest pathogen control measure, particularly in ensuring optimal quality and extending the shelf life of strawberries.

Keywords: Bacterial pathogen, Food safety, Fungal pathogen, Pathogen inactivation, Postharvest quality, Reactive species

1 Introduction

Strawberries (*Fragaria x ananassa*) are considered one of the most economically significant fruits worldwide. In 2023, their total global production exceeded 10 million tons, with Asia being the largest continental producer, followed by America and Europe [1]. Strawberries are highly perishable and prone to fungal and bacterial pathogens during cultivation, transportation, and postharvest storage, which can reduce their shelf life and market value. They last 1 to 2 days at room temperature and about 7 days at 5 °C due to their delicate skin and soft flesh [2], [3]. Fungal pathogens, including *Botrytis cinerea*, *Rhizopus* spp., *Mucor* spp., *Colletotrichum* spp., and *Penicillium* spp., are of particular concern [4], [5]. Additionally, bacterial pathogens such as *Salmonella* spp., *Escherichia coli*, *Listeria monocytogenes*, and *Staphylococcus* spp. pose a significant risk in the postharvest management of strawberries [6], [7].

To address these issues, control methods have undergone significant improvements. However, many of these techniques primarily rely on chemical treatments, which have drawbacks, particularly chemical residues, resistance development, and environmental concerns, leading to increased interest in exploring more sustainable and efficient pathogen inactivation methods.

Recently, the use of the advanced oxidation processes (AOPs) for pathogen inactivation, particularly in agricultural applications, has been widely studied. AOPs generate highly reactive species, including hydroxyl radicals and ozone, which exhibit potent antimicrobial activity [8]. These include plasma-activated water (PAW), which is produced by exposing water to cold atmospheric plasma. Optimizing PAW generation involves controlling parameters such as plasma-forming voltage, carrier gas composition, temperature, treatment duration, and frequency. Studies attribute the significant antimicrobial properties of PAW to its generation of diverse reactive oxygen and nitrogen species (RONS) [9].

Similarly, nanotechnology has also gained interest as an emerging science, offering significant potential in the preservation of fruits and vegetables. Researchers have characterized micro-nano bubbles (MNBs) as nanoscopic gaseous cavities sized at the micro and nanoscale, having longer stability in aqueous solution and a large specific surface area [10], [11]. MNBs have been studied for their unique physiochemical properties, recognizing their applicability in managing the postharvest quality of agricultural produce. Additionally, their ability to improve the water and gas exchange at the cellular level offers the potential to reduce spoilage and maintain the overall quality of fruits and vegetables.

To further investigate the potential of PAW and MNBs in controlling pathogens on strawberries, this review article examines the various fungal and bacterial pathogens that affect their postharvest quality. It also highlights the existing pathogen control methods, including chemical, physical, and biological treatments. Additionally, it aims to explore the application principles of PAW and MNBs in agricultural postharvest management and discuss future aspects and research areas for consideration.

2 Fungal Pathogens in Strawberry Fruit

Strawberries are susceptible to pathogens, including fungi, bacteria, and viruses. Among these, fungal infections are the most economically impactful, as they can infect leaves, roots, crowns, and fruits. Fungal pathogens are considered primary contributors to postharvest diseases in strawberries, with their presence in fruits leading to estimated losses ranging from 20% to 50% [12]. These can also cause losses throughout various stages, such as handling, transportation, and significantly during storage [13], [14]. Furthermore, specific fungal pathogens pose a risk to human health due to their ability to produce mycotoxins, such as those produced by *Aspergillus niger* and *Penicillium expansum* [15]. The severity of fungal infections depends on the cultivar and environmental conditions. Chandler, Camarosa, and Seascape cultivars are known to be vulnerable to *Botrytis cinerea* (gray mold) and *Colletotrichum* spp. (anthracnose) [16], [17]. Moreover, environmental conditions such as humidity and temperature, along with fruit handling practices and the fruit's physiological status, significantly influence the extent of damage [13].

Table 1 presents the list of strawberry diseases and their corresponding fungal pathogens. In particular, most of these pathogens exhibit necrotrophic behavior, meaning that they can destroy host cells by secreting cell wall-degrading enzymes or toxins, subsequently absorbing nutrients from the dead cells.

Table 1: Fungal pathogens of strawberries.

Genus	Species	Strawberry Disease	Ref.
Alternaria	*tenuissima*	*Alternaria* fruit rot	[18]
Aspergillus	*niger*	*Aspergillus* fruit rot	[19]
Botrytis	*cinerea*	Gray mold, *Botrytis* fruit rot	[20], [21]
Cladosporium	*cladosporioides*	*Cladosporium* fruit rot	[22]
Colletotrichum	*acutatum*	Anthracnose fruit rot, crown rot, black spot	[23], [24]
	gloeosporoides	Anthracnose fruit rot, crown rot	[24]
Colletotrichum	*fragariea*	Anthracnose fruit rot, crown rot, black spot	[24]
	siamense	Anthracnose crown rot	[24]
	fructicola	Anthracnose fruit rot	[24]
	gloeosporioides	Anthracnose fruit rot, crown rot	[24]
	aenigma	Anthracnose crown rot	[24]
Fusarium	*sambucinum*	Fruit blotch	[25]
Gnomonia	*comari*	Stem end rot, leaf blotch	[26]
Mucor	*hiemalis*	*Mucor* fruit rot	[27]
	mucedo	*Mucor* fruit rot	[27]
	piriformis	*Mucor* fruit rot	[27], [28]

Table 1: (continued).

Genus	Species	Strawberry Disease	Ref.
Mycosphaerella	*fragariae*	Black seed disease	[29]
Neopestalotiopsis	*rosae*	Crown rot	[30]
Pestalotia	*longisetula*	*Pestalotia* fruit rot	[31]
Penicillium	*cyclopium*	*Penicillium* fruit rot	[31]
	digitatum	*Penicillium* fruit rot, green mold	[32]
	expansum	*Penicillium* fruit rot, blue mold	[33]
Peronospora	*potentillae*	Downy mildew, fruit blotch	[34]
Phytophthora	*cactorum*	Leather rot	[35]
	citrophthora	Leather rot	[36]
	nicotianae	Leather rot	[37]
Rhizoctonia	*fragariae*	Anther, pistil blight	[38]
	solani	Hard brown rot	[39], [40]
Rhizopus	*stolonifer*	*Rhizopus* rot	[41]
	sexualis	*Rhizopus* rot	[41]
Schizoparme	*straminea*	Fruit blotch	[42]
Sclerotinia	*sclerotiorum*	*Sclerotinia* crown, fruit rot	[43]
Sclerotium	*rolfsii*	Southern blight, fruit blotch	[44]
Sphaerotheca	*macularis*	Powdery mildew	[45]

Several postharvest pathogens, including *Alternaria* spp. and *Colletotrichum gloeosporioides*, can infect strawberries before harvest. These pathogens often remain dormant during the fruit's growth and development but become necrotrophic upon ripening or senescence [46]. Significant biochemical changes during fruit maturation trigger the reactivation of these compounds, closely linked to the fruit's physiological state. Moreover, diseases such as anthracnose, gray mold, transit rot, green mold, and blue mold exhibit a quiescent phase of infection. These occur when the disease develops during or after harvest, typically through penetrating wounds on the fruit [47].

Globally, researchers identify *Botrytis cinerea* and *Colletotrichum* spp. as major pathogens responsible for severe strawberry fruit diseases. These pathogens significantly contribute to fruit losses and account for the highest quantity of fungicides applied in strawberry production. Consequently, the use of these treatments results in substantial financial expenditures for farmers, representing a significant burden on the strawberry industry across many countries [42]. On the other hand, *Rhizopus* spp., *Mucor* spp., and *Penicillium* spp., commonly found in strawberries, contribute to postharvest decay but have a comparatively lesser impact on the need for chemical treatments [48]. Table 2 summarizes the major fungal pathogens commonly associated with postharvest disease in strawberries, including *Botrytis cinerea*, *Rhizopus* spp., *Mucor* spp., *Colletotrichum* spp., and *Penicillium* spp.

Table 2: Common fungal pathogens of strawberry fruit and their symptoms.

Pathogen	Symptoms	Ref.
Botrytis cinerea	Light brown lesions, loss of fruit firmness	[49], [50]
Rhizopus spp.	Tissue severely decayed, juice released	[51]
Mucor spp.	Fruit tissue becomes very soft, leak sticky red juices	[52]
Colletotrichum spp.	Small, dark, and sunken lesion	[53]
Penicillium spp.	Small water-soaked lesions	[54]

2.1 *Botrytis cinerea*

Botrytis cinerea is a typical necrotrophic, polyphagous pathogen that belongs to the phylum Ascomycota and is capable of infecting seedlings and fruits. It affects more than 1,400 species of host plants; hence, it is ranked second among pathogenic fungi [42], [49]. Specifically, gray mold, attributed to *Botrytis cinerea*, is considered the primary disease of strawberry fruit. This fungal species can cause damage under moist and humid conditions, which favor fungal growth. The pathogen primarily affects fruit, but can also colonize leaves, flowers, and stems. It survives partly by forming sclerotia, a dense mass of fungal tissue that functions as a survival structure under unfavorable conditions. Sclerotia remain in plant debris, soil, or crop bedding and germinate when environmental conditions become favorable [49], [55], [56].

B. cinerea can be observed at all growth stages of strawberries, but the symptoms are typically visible during the postharvest stage. It thrives in moderate temperature ranges of 15 °C to 25 °C but can grow at 0 °C [20]. This adaptability to various environmental

conditions makes the pathogen particularly challenging to manage [57]. A recent study by Yousef *et al*. examined ten *B. cinerea* isolates and identified isolate B3 as the most potent, while isolate B5 exhibited a low level of pathogenicity. Researchers observed a positive correlation between this variability and oxalic acid production, a key factor contributing to the pathogenicity of *B. cinerea*. Additionally, it exhibits a high degree of genetic variability and adaptability that contributes to its widespread resistance to various control methods [21].

Figure 1 illustrates the disease cycle of *Botrytis cinerea* in strawberries. It starts with the presence of sclerotia on dried leaves or plant debris within the field, which release ascospores. These spores germinate on leaves and flowers, followed by a symptomless quiescent state [58], [59]. Based on the study of Petrasch *et al*., after flower infection, *B. cinerea* tends to remain quiescent due to proanthocyanins that inhibit the activity of fungal enzymes, such as polygalacturonases. Fungal infection is activated when environmental conditions become optimal [59].

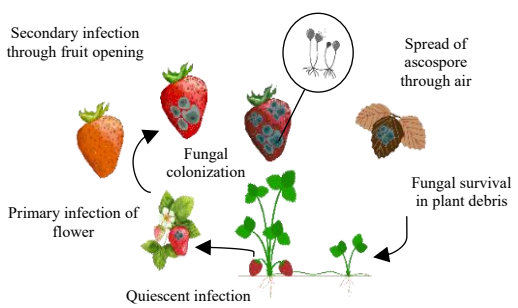

Figure 1: Schematic diagram of the disease cycle of *Botrytis cinerea* in strawberry

B. cinerea infects host plants through wounds, stomata, or direct penetration. Its oval conidia germinate on the plant surface in the presence of external nutrients. Optimal infection occurs under humid conditions and temperatures ranging from 10 °C to 25 °C. To effectively infect host tissue, *B. cinerea* secretes a variety of virulence factors, including enzymes that degrade plant cell walls, proteins that induce cell death, and phytotoxic compounds such as sesquiterpene botrydial and polyketide botcinins. *B. cinerea* also produces oxalic acid, which lowers the pH of infected tissues, thereby facilitating the activation of fungal enzymes such as proteases, pectinases, and laccases that contribute to tissue breakdown. Additionally, it releases immune-suppressing molecules, such as small ribonucleic acids (sRNAs), which are exchanged between the pathogen and the plant during host-pathogen interactions, influencing disease progression. Researchers have found that sRNAs from *B. cinerea* regulate defense-related genes in *Arabidopsis*, thereby influencing the severity of infection [21], [60].

2.2 *Rhizopus* spp.

Rhizopus spp. is a filamentous black bread fungus that causes soft rot, black mold, and *Rhizopus* rot in strawberries [61], [62]. It consists of branched, non-septate white hyphae measuring 900 to 2700 µm in length and 22 to 32 µm in diameter. Its sporangium is spherical, initially white, and then turns black as it matures. The sporangium contains many spores, most of which are 90 to 120 µm in length [51]. Researchers characterized *Rhizopus* spp. by its fast growth and production of coarse, cottony, white to grayish-black mycelium [63], [64]. According to Liu *et al.,* the pathogenicity and infection mechanism of *Rhizopus* spp. remain active over a wide range of temperatures, with an optimum of 25 °C. Its spores and mycelia typically spread through the wounds of fruit when the temperature exceeds 5 °C, with symptoms of infection appearing within 24 to 48 h. During germination, *Rhizopus* spores release various amino acids, enzymes, and other proteins, including polygalacturonase and pectin methylesterase. These enzymes facilitate the contamination of the host's injured tissues by breaking down cell wall components, leading to rapid digestion of the host cells, electrolyte leakage, and subsequent decay [51].

As depicted in Figure 2, the disease cycle of *Rhizopus* spp. in strawberries begins with contaminated plants or field debris. Fungal spores are produced and disseminated by the wind. These conidia subsequently infect the flowers of strawberry plants, leading to the infection of green to mature fruits. When conditions become favorable, the fruit becomes visibly covered with fuzzy conidial masses, indicating active fungal growth.

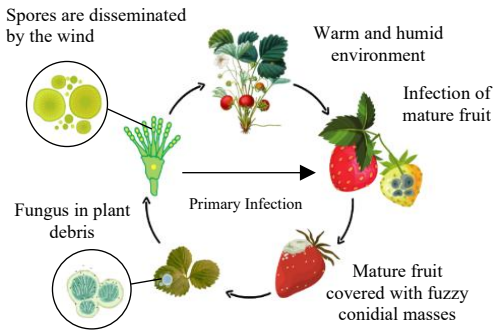

Figure 2: Schematic diagram of the disease cycle of *Rhizopus* spp. in strawberry.

Specifically, the germination of *R. stolonifer* spores requires specific nutrients. With adequate external sources of carbon and nitrogen, the spores will begin to germinate and develop infectious mycelia within 3 to 5 hours. Symptoms appear within a day, with rapidly growing mycelium forming fibrous gray sporangia that cover the infected fruit. As decay progresses, the tissue softens and breaks down into a watery decay, eventually releasing a fermented or acidic odor within 2 to 3 days [51], [65].

2.3 *Mucor* spp.

Mucor spp. is a genus of fungi that belongs to the order *Mucorales*, a saprobic and facultative phytopathogenic fungus that causes soft rot in strawberries [66]–[68]. Mucor mold infestation is most prevalent in crops with fruit that have sustained injuries during pollination stages, such as strawberries. Researchers associated *Mucor* spp. infection with the enzymatic activity of its polygalacturonases, which degrade the middle lamellae of plant cells. Along with xylanase, cellulase, and amylase, polygalacturonases act as macerating enzymes that soften fruit tissues [48].

Mucor spp. colonizes on decaying organic matter and can infect strawberries through even the slightest wound, rapidly causing fruit decay [69], [70]. It is found naturally in soil and plant debris and can be dispersed through the wind [71], [72]. This pathogen generally thrives at temperatures between 5 °C and 25 °C. Optimal growth is often observed around 20 °C, while temperatures above 30 °C can inhibit its growth. However, some species, like *Mucor indicus*, are thermotolerant and can withstand higher temperatures [66], [73].

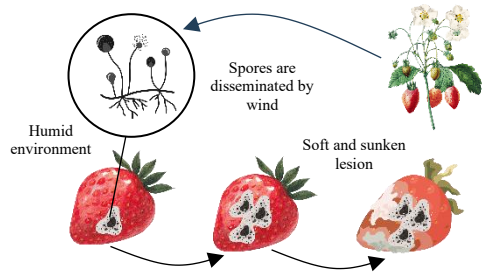

Figure 3: Schematic diagram of the disease cycle of *Mucor* spp. in strawberry.

Figure 3 presents the disease cycle of *Mucor* spp. in strawberries, which begins when the fungus infects the fruit through natural openings or wounds on its surface. Once inside, the fungus rapidly colonizes the fruit, secreting enzymes that break down the tissue and cause it to rot, resulting in liquefaction of the entire fruit. Under high humidity conditions, the infected fruit develops a dense, wiry mycelium, with black sporulation appearing at the ends of elongated spore-bearing structures, which release spores into the environment. These spores can spread to other fruits, particularly in late summer.

Mucor spp. and *Rhizopus* spp. rots exhibit the same characteristics, making it challenging to distinguish between the two in field conditions. Although the fruit-softening symptoms may appear very similar, researchers identify these fungi by observing the fungal growth under a hand lens. Sporangia, tiny, dark brown to black spherical structures, can be found at the ends of white fungal strands. In particular, *Rhizopus* produces dry sporangia that appear randomly distributed, whereas *Mucor* forms wet sporangia aligned in parallel strands with a viscous liquid film [48].

2.4 *Colletotrichum* spp.

Colletotrichum spp. can cause anthracnose, a detrimental fungal disease that results in a 70% yield loss in strawberries [53], [74], [75]. It is typically found at the crown of the fruit, which is why it is often called crown rot. It has three related species, namely *C. acutatum*, *C. gloeosporioides*, and *C. fragariae*. Specifically, *C. acutatum* is known for causing severe fruit rot, while *C. gloeosporioides* and *C. fragariae* are pathogens affecting the fruit crown [16], [76].

In the study by Ureña-Padilla *et al*., researchers isolated *Colletotrichum* spp. from diseased strawberry fruit and crowns. Only *C. acutatum* was recovered

from the fruit itself, and *C. gloeosporioides* was isolated from the fruit crown, which caused the collapse and death of the plant [76]. Additionally, a study by Guidarelli *et al*., demonstrated that after 24 h of interaction with *C. acutatum*, white strawberry fruits exhibited quiescence marked by melanized appressoria, whereas red fruits showed evidence of necrotrophic infection. Microarray data further revealed the upregulation of genes associated with epi/catechin pathways and fatty acid metabolism, a key process in the biosynthesis of quiescence-related compounds like flavan-3-ols, proanthocyanidins, and antifungal dienes, suggesting that these serve as defense components during strawberry ripening [77].

As depicted in Figure 4, once the conidia land on the host, they will germinate and form appressoria, then subsequently penetrate the epidermal cells. *Colletotrichum* spp. can overwinter in plant debris, notably in decayed fruit, and produce primary inoculum during the spring. Optimal conditions for disease development occur at approximately 27 °C, though the fungus is capable of infecting fruit at lower temperatures. Lesions, characterized by the production of conidia, can trigger the infection cycle throughout the growing season. Conidia formation follows an infection latency period of 7 to 11 days at 5 °C and 2 to 3 days at 25 °C. While conidial production occurs across a temperature range of 5 °C to 35 °C, it is most prolific at temperatures between 22 °C and 26 °C. Conidial dispersal primarily occurs through rain, insects, animals, and human activities such as those of farm workers. Although *C. acutatum* exhibits a broad host range encompassing numerous fruit, vegetable, and weed species, existing research indicates that the strains pathogenic to strawberries show a relatively high degree of host specificity [24], [78], [79].

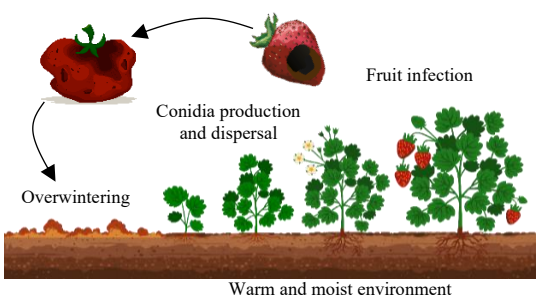

Figure 4: Schematic diagram of the disease cycle of *Colletotrichum* spp. in strawberry.

Understanding the mechanisms by which *Colletotrichum* spp. interacts with strawberry fruit at different ripening stages is essential for developing strategies for effective disease management. The different responses observed in white and red strawberries, as well as the specific dense-related genes, suggest that ripening-induced defense compounds play a significant role in mitigating the pathogenic infection.

2.5 *Penicillium* spp.

Penicillium fruit rot, primarily caused by *Penicillium expansum* along with other *Penicillium* species, is one of the major pathogens responsible for the postharvest decay of strawberries [48]. Several *Penicillium* species have been documented as producers of aflatoxins and ochratoxins, which can negatively affect the health of consumers [54], [80]. Infection may occur during fruit ripening, harvest, storage, and transport, leading to spoilage, financial losses, and, in some cases, the production of health-threatening mycotoxins [80]. In the study by Liu *et al*., researchers examined 91 strains of *P. expansum* and identified six mycotoxins, with patulin (PAT) and chaetoglobosin A being the most prominent, found at average concentrations of 77.56 $mg \cdot kg^{-1}$ and 45.58 $mg \cdot kg^{-1}$, respectively. Using untargeted metabolomics, the researchers profiled 506 metabolites, observing a general decrease in primary metabolites during fungal cultivation as *P. expansum* assimilated them. A comparative analysis between samples with high and low PAT levels revealed unique metabolic fingerprints. This distinct metabolic signature, particularly in organic acids, benzenoids, and organoheterocyclic metabolites, was directly linked to mycotoxin production pathways [81].

This fungal pathogen is characterized by the appearance of blue-green spore masses on the infected fruit, which initially present as light to dark-brown circular lesions [82]. Studies have found that the continuous application of fungicides against gray mold can contribute to the occurrence of *Penicillium* fruit rot [48]. Generally, it thrives at temperatures ranging from 25 °C to 30 °C, but it can still grow at cooler temperatures, especially in the range of 4 °C to 20 °C [6].

In the related study by Hussein *et al*., the authors examined the pectinase activity of *Penicillium citrinum*, highlighting its role in breaking down fruit tissue and causing rot. Their findings revealed that *P.*

citrinum isolates demonstrated significant production of various pectinolytic enzymes, including polygalacturonases and pectin methyl esterases, both in liquid culture and when inoculated onto fruit. This enzymatic activity was directly correlated with the observed fruit softening and tissue maceration, confirming the crucial role of these enzymes in the pathogen's ability to degrade the cell walls of strawberry fruit and cause decay. It highlights a key mechanism by which *Penicillium* species induce spoilage [83].

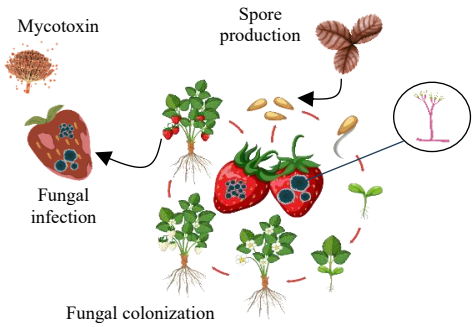

Figure 5: Schematic diagram of the disease cycle of *Penicillium* spp. in strawberry

As illustrated in Figure 5, the disease cycle of *Penicillium* decay in strawberries begins with the production of inoculum. *Penicillium* fungi produce spores on infected strawberry fruit, soil, or debris. These spores can be dispersed through various means, including water, wind, or insects, infecting new strawberry plants. Infection occurs when spores come into contact with wounded or intact strawberries, colonizing the fruit and breaking down cell walls. The colonization process is facilitated by the production of enzymes and toxins that enable the fungus to penetrate and degrade the fruit's cellular structure. As the fungus grows, it produces new spores on the infected fruit, which can infect others or spread to different areas. This continuous cycle of infection, colonization, and sporulation enables *Penicillium* decay to spread rapidly, causing significant damage to strawberry crops [84].

The widespread impact of *Penicillium* fruit rot highlights the significant challenges of managing postharvest diseases in strawberries. Since some strains can produce mycotoxins, future research should integrate both controlling fungal growth and the production of mycotoxigenic strains.

3 Bacterial Pathogens in Strawberry Fruit

Strawberries carry a diverse range of microorganisms, which can impact their shelf life and quality [2]. Aside from fungal pathogens, bacterial pathogens are another type of microbiota considered spoilage organisms [2], [85]. In recent years, multiple foodborne outbreaks have been linked to strawberries, with particular concern for human pathogenic bacteria [86]. Some contaminants are considered detrimental and can cause serious illnesses [2].

A study conducted by Tenea *et al*. identified bacterial families, including *Pseudomonaceae*, *Yersiniaceae*, and *Hafniaceae,* as prevalent in the collected strawberries. Their findings suggest that microbial composition varies depending on the sample source and fruit variety. Researchers detected *Escherichia coli* and *Salmonella enterica* in ready-to-eat strawberries from both field and market sources, highlighting potential food safety concerns. Interestingly, *Shewanella putrefaciens* and *Shewanella profunda*, two opportunistic human pathogens, were found exclusively in market samples, suggesting possible contamination during handling and distribution. Additionally, researchers observed that microbial compositions are significantly influenced by fruit ripeness and postharvest conditions [2].

Table 3: Bacterial pathogens of strawberries.

Genus	Species	Strawberry Disease	Ref.
Xanthomonas	*fragariae*	Angular leaf spot, lesion in fruit calyx	[87]
	arboricola	Bacterial leaf blight, fruit rot	[88]
Pseudomonas	*fragariae*	Leaf spot, fruit rot	[89]
Escherichia	*coli*	Foodborne illnesses	[2]
Enterococcus	*gallinarum*	Foodborne illnesses	[2]
Salmonella	*enterica*	Foodborne illnesses	[90]
Listeria	*monocytogenes*	Foodborne illnesses	[91]
Bacillus	*cereus*	Foodborne illnesses	[92]
Staphylococcus	*aureus*	Foodborne illnesses	[93]
	epidermidis	Foodborne illnesses	[93]
Shewanella	*putrefaciens*	Foodborne illnesses	[2]
	profunda	Foodborne illnesses	[2]

Several studies have documented the occurrence of bacterial pathogens in strawberry fruits, both in the field and in storage. Specifically, Table 3 presents the isolated bacterial species and their corresponding diseases.

Among the bacterial pathogens, human pathogenic bacteria such as *Salmonella* spp., *Escherichia coli, Listeria monocytogenes*, and *Staphylococcus* spp. are the most prevalent [94], [95].

3.1 *Salmonella* spp.

Salmonella spp. is a gram-negative, rod-shaped bacterium within the *Enterobacteriaceae* family [96], [97]. It is facultatively anaerobic and non-sporulating, which makes it a significant contributor to the global burden of foodborne diseases [98]. Specifically, there are over 2,600 *Salmonella* serotypes, with Enteritidis, Typhimurium, Newport, Javiana, and Heidelberg being the most commonly detected [99]. This bacterium can proliferate in various food products and remain viable even after freezing or drying, retaining its pathogenic potential. Additionally, studies indicate that *Salmonella* can survive in highly saline environments [100].

Salmonella spp. thrives in strawberry fruit at 25 °C, while refrigeration at 4 °C significantly reduces its growth [98], [101]. In a broader sense, this mesophilic bacterium can grow in temperatures ranging from 5 °C to 46 °C, with an optimum growth temperature between 35 °C and 37 °C. It is unable to multiply at a water activity (a_w) of 0.94, especially when combined with a pH of 5.5 or lower, and is less tolerant of a pH of 4.5 and below [98], [102]. On the other hand, it grows in low a_w with a pH range of 4 to 9, with 6.5 to 7.5 being ideal [103].

Tenea and Reyes reported the presence of *Salmonella enterica* in ready-to-eat strawberries collected from both farm fields and retail stands, with higher contamination in market-sourced samples [2]. Their findings linked postharvest handling and retail exposure to an increase in pathogenic bacterial loads. Additionally, a separate study evaluating the survival and biofilm formation of *S. enterica* serovar Thompson on strawberries stored at 4 °C, 7 °C (192 h), and 20 °C (72 h) showed a population decline of 2.0, 1.7, and 2.0 log CFU/g, respectively, from an initial inoculum of ~5 log CFU/g. Biofilms were observed on the epidermis at all temperatures, indicating a persistence strategy under storage stress conditions [98].

3.2 *Escherichia coli*

Escherichia coli is a straight, rod-shaped bacterium, measuring approximately 1 to 3 μm in length and 0.4 to 0.7 μm in width. It can survive in temperatures ranging from 10 °C to 40 °C, with an optimal growth temperature of 37 °C and a pH range of 4.5 to 9.5 [104]. While most *E. coli* strains are non-pathogenic, specific variants, such as Shiga toxin-producing *E. coli* (STEC), are associated with foodborne illnesses [105]. Among these, *Escherichia coli* O157:H7 is widely recognized as a foodborne pathogen, followed by serotypes O104:H4 [106].

Recent studies have identified *E. coli* contamination in ready-to-eat strawberries from both agricultural fields and commercial markets [2], [107]. Contaminated agricultural water has also been identified as a source of pathogenic contamination. However, ensuring the adequate and sanitary quality of agricultural water (<1 CFU /100 mL) during postharvest operations, such as washing, can be challenging. In the study of Vesga *et al., E. coli* was detected in 12.5% of strawberry samples irrigated with surface water. These findings were based on samples collected from farms, markets, and supermarkets. The study highlighted the persistence of *E. coli* across the strawberry supply chain, underscoring the vulnerability of strawberries to fecal contamination due to irrigation sources [107].

Escherichia coli O157:H7 has been observed on the surface and within the pulp of strawberry fruits throughout production and postharvest stages [105], [106]. A study by Yu *et al.,* examined the survival of *E. coli* O157:H7 on strawberries, a fruit that is typically unwashed during production and handling. Two bacterial strains were tested, both on the surface and inside the fruit. Results showed that *E. coli* survived both externally and internally at 23 °C for 24 hours and at 10 °C, 5 °C, and -20 °C for three days. The highest bacterial reduction occurred at -20 °C and on the fruit surface when refrigerated, while bacteria inside the fruit tended to survive better [108]. Moreover, Knudsen *et al.* investigated the survival of *E. coli* O157:H7 on fresh and frozen strawberries. Their findings indicate that these pathogens can survive on fresh strawberries throughout their expected shelf life and remain viable in frozen storage for over a month, with population reductions varying in conditions and in the presence of sucrose [109].

3.3 *Listeria monocytogenes*

Listeria monocytogenes is a gram-positive bacterium with a rod-shaped structure commonly present in the environment. It typically measures between 0.5 and 2 μm in width and 0.5 and 4 μm in length. This pathogen is responsible for listeriosis, a serious foodborne illness. It is remarkably resilient, capable of surviving and proliferating within a temperature range of -0.4 °C to 45 °C, across pH levels from 4.6 to 9.5, and in an environment with low water activity (a_w<0.90). Additionally, it demonstrates high salt tolerance, with concentrations up to 20% [110], [111].

L. monocytogenes is capable of surviving and replicating within the host cells. This characteristic enables the bacteria to evade the host's immune response and cause systematic infection [112], [113]. The bacterium is commonly found in soil and plant debris and is particularly prevalent in fruits and vegetables that grow directly in contact with the soil, such as strawberries [114].

Research by Yin *et al*., investigated the persistence of *L. monocytogenes* on fresh strawberries during refrigerated storage. Their findings revealed that the pathogen can survive for several days at a temperature of 4 °C. In untreated control samples, *L. monocytogenes* populations remained relatively stable for 7 days, indicating that strawberries provide a suitable surface for short-term survival under cold conditions. Although lactic acid bacteria (LAB) treatment significantly reduced pathogen levels, the research underscores that *L. monocytogenes* can survive on strawberry surfaces during typical postharvest storage [91].

3.4 *Staphylococcus* spp.

Staphylococcus spp. is a gram-positive, spherical bacterium that typically ranges in diameter from 0.5 to 1.5 μm [115]. The growth and toxin production of *Staphylococcus* spp. is optimal in the presence of oxygen, though it is capable of growing anaerobically [116]. It is known for its characteristic arrangement in grape-like clusters, a result of division in multiple planes. Unlike rod-shaped bacteria, it maintains a coccus morphology, which contributes to its resilience and ability to colonize various environments [117]. Specifically, *Staphylococcus aureus* can survive a temperature range of 7 °C to 48.5 °C. It thrives in pH conditions between 7.0 and 7.5, with survival limits extending from a minimum of 4.2 to a maximum of 9.3. While it can survive in foods with a pH of 4.2, it remains dependent on the type of acid present [118]. Notably, *Staphylococcus* spp. is highly resistant to drying and capable of both growth and enterotoxin production in foods with water activity (a_w) levels as low as 0.85 [119].

Staphylococcus species can contaminate crops during cultivation through contact with soil, water, and handling by farm workers. Studies have found that *Staphylococcus aureus* and *Staphylococcus epidermidis* are present in strawberry fruits [93]. Yoon *et al.* conducted a microbiological assessment for bacterial contamination in tunnel-style strawberry greenhouses and packaging centers. *S. aureus* showed high bacterial counts across most samples, indicating significant contamination risks associated with strawberry handling and processing [120]. In the study of Kim *et al*., the authors also detected *S. aureus* contamination in 16% of collected samples from the assessed strawberry farm, with the highest occurrences found on employees' hands, scissors, and strawberries. A polymerase chain reaction (PCR) analysis of *S. aureus* enterotoxin genes shows that 92% of strains carried Staphylococcal enterotoxin A (SEA), while 38% carried Staphylococcal enterotoxin B (SEB), and Staphylococcal enterotoxin C (SEC) was not found. These findings highlight the presence of toxin-producing *S. aureus* strains in the strawberry production environment [121]

4 Existing Pathogen Control for Strawberries

Strawberries are highly susceptible to pathogen contamination, requiring effective control strategies to maintain food safety and postharvest quality. Several studies have explored pathogen control methods, providing insight into various techniques and changes in the pathogenicity of target organisms. This section discusses existing pathogen control methods, focusing on chemical, physical, and biological treatments. Specifically, Table 4 presents the comparative analysis of existing pathogen control methods, focusing on their efficacy, cost, and limitations.

Table 4: Efficacy, cost, and limitations of existing pathogen control methods for strawberries.

Category	Pathogen Control	Efficacy	Cost	Limitations	Ref.
Chemical	Chemical fungicide	Demonstrated significant bacterial reduction.	Moderate: Cost varies depending on concentration and volume.	• Higher concentration can negatively impact fruit quality. • Residual chemical toxins are linked to environmental problems and adverse health effects.	[32], [108], [122]
	RNA-based fungicide	Reduces fungal bacteria, particularly *Botrytis cinerea*	High (Initial): Currently in research and development phase; high upfront investment expected for commercialization.	Potential for off-target effects and resistance development.	[123], [124], [125]
	Melatonin treatment	Optimizing melatonin concentration can reduce pathogenicity and enhance postharvest fruit quality.	Low: Relatively inexpensive cost for synthesized melatonin.	• Limited commercial availability. • Optimal concentration and timing are still under study.	[20]
Physical	MAP	Reduces microbial growth and slows down spoilage processes.	Moderate: Primarily involves the cost of specialized packaging materials and equipment.	It may not completely eliminate pathogens, only inhibit their growth.	[126], [127]
	Cold Storage	Broad-spectrum microbial control, decay mitigation, and fruit quality preservation.	High (Initial): Significant upfront investment in equipment.	Limited in penetration; only long-lived species reach the fruit.	[128]
	Isochoric impregnation	• Cause smaller weight loss for fruits. • Extend shelf life and prevent microbial contamination.	Moderate to high cost: Requires specialized equipment.	• Requires specific equipment and setup to maintain constant volume. • Involves customizing the impregnation substance.	[86]
Biological	Bio-fungicides	• Exhibit antagonistic properties by competing for nutrients and space, exerting antibiosis effects, and triggering the resistance mechanism of the pathogen. • Effective against a range of fungal and bacterial diseases.	Moderate to High: It varies by agents and application techniques.	Performance varies under field conditions.	[47]
	Plant extracts	Contains various bioactive compounds that exhibit antimicrobial properties.	Low to Moderate: Varies widely depending on plant source and extraction method. Some can be low cost for growers (e.g., agricultural waste) while commercial formulation has a moderate investment cost.	Potential phytotoxicity at high concentrations.	[55]

4.1 *Chemical treatment*

A study by Acosta-González *et al*., evaluated the preventive and curative efficacy of various chemical treatments against *Neopestalotiopsis rosae*, the causative agent of crown rot. Among the tested chemical fungicides, including prochloraz, cyprodinil with fludioxonil, and pydiflumetofen with fludioxonil, preventive applications of these agents demonstrated the highest disease suppression, achieving 99 to 100% efficacy in reducing disease incidence and severity. In contrast, curative treatments showed markedly lower effectiveness, with most failing to exceed a 37% control threshold [122].

On the other hand, the external application of RNA interference (RNAi)-based fungicides has also been explored to control pathogen contamination in strawberries. RNAi-based fungicides target specific genes in phytopathogens, which prevents their spread [123]. Sabbadini *et al*., demonstrated that double-stranded RNAs (dsRNAs) targeting *Botrytis cinerea* effectively downregulated *Bc-DCL* gene expression, leading to reduced pathogenicity and fungal growth [124]. The application of dsRNA and single-stranded RNA (ssRNA) molecules to strawberry surfaces also proved effective in preventing gray mold infection [125].

Additionally, a study by Promyou *et al*. examined the effects of exogenous melatonin treatment on postharvest quality and disease resistance of strawberry fruits against *Botrytis cinerea*. The findings suggest that optimizing melatonin concentration can reduce infection rates of inoculated pathogens [20].

However, despite their effectiveness, chemical treatments pose potential risks. Residual chemical toxins in strawberries have been linked to adverse health effects, such as endocrine disturbances and neurological disorders. Additionally, certain fungicides have been found to alter the metabolic pathways of strawberries, resulting in changes in flavor and nutritional value [129], [130].

4.2 *Physical treatment*

Modified atmosphere packaging (MAP) has been widely studied as a method to extend the shelf life of strawberries. Research indicates that equilibrium-modified atmosphere packaging (EMAP) can significantly enhance postharvest quality and antioxidant activity by regulating oxygen (O_2) and carbon dioxide (CO_2) concentrations, thereby reducing microbial growth and slowing down spoilage processes [126]. Lei *et al*., found that an optimal atmosphere of 10 kPa O_2 + 10 kPa CO_2, maintained by microporous polyethylene film, increased polyphenol accumulation, thereby improving antioxidant properties and extending shelf life by several days. Additionally, polyethylene packaging under a modified atmosphere has been shown to influence metabolic changes in strawberries, reducing spoilage biomarkers such as oxidized phosphatidylcholines and lyso-phosphatidylcholines [127].

Steinka & Kukulowicz investigated the presence and behavior of methicillin-resistant *Staphylococcus aureus* (MRSA) in fresh and frozen strawberries, assessing how different freezing methods affect bacterial contamination. Fresh and frozen strawberries were tested for MRSA, with samples divided into washed and unwashed groups. *Staphylococcus aureus* and *Staphylococcus epidermidis* were inoculated into the samples, which were then stored at -18 ± 2 °C for two months. The study concluded that MRSA was present in 15.4% of field-obtained strawberries, and freezing at -18 °C reduced *S. aureus* and *S. epidermidis* levels by 0.16 and 0.47 $\log_{10}$ CFU/g, respectively, after rinsing [128].

However, freezing can cause cellular damage, resulting in moisture loss and a decline in sensory attributes such as firmness and juiciness. Prolonged exposure to modified atmospheres may also accelerate anthocyanin degradation, leading to discoloration and reduced consumer acceptance. While many studies on MAP aim to preserve anthocyanins and fruit color, optimal gas composition and exposure duration are critical. If the conditions are suboptimal for a specific fruit's tolerance, the protective effects of MAP can diminish, and anthocyanin degradation can accelerate, leading to undesirable outcomes [131]–[133].

4.3 *Biological treatment*

Biological control agents (BCAs), primarily composed of bacteria and yeast, play a crucial role in mitigating postharvest spoilage in strawberries. They exhibit antagonistic properties against pathogens by competing for nutrients and space, effectively limiting the resources available for microbial growth. Additionally, BCAs exert antibiosis effects by producing volatile or toxic compounds that disrupt the survival of pathogens. Some of these agents can also trigger resistance mechanisms within the host tissue, which strengthen the fruit's natural defenses [134]. Several commercially available biofungicides are widely utilized for pathogen control. Notable examples include *Pseudomonas syringae*, *Bacillus subtilis*, *Candida sake*, and *Metschnikowia fructicola* [47].

A study by Zhao *et al*., examined the effectiveness of *Debaryomyces hansenii* as a biocontrol agent for combating postharvest diseases in strawberries. The research found that treating strawberries with *D. hansenii* helped inhibit natural decay and maintain a higher ascorbic acid content, a key indicator of quality. The study revealed that *D. hansenii* alters the microbial diversity on the surface of strawberries. Specifically, it changes the composition and structure of the fungal community,

which in turn helps inhibit plant pathogens and reduces the occurrence of postharvest diseases [134]. Moreover, the study by Kahramanoglu *et al*., investigated the antifungal effects of *Origanum onites* L. and *Ziziphora clinopodioides* L. essential oils against *Botrytis cinerea* in strawberries. *In vitro* tests using the poisoned food technique showed potent mycelial inhibition at optimal doses, while *in vivo* vapor treatments effectively prevented gray mold with moderate effects on fruit weight loss and quality [55].

While BCAs offer promising pathogen control, resistance development remains a potential concern. Some pathogens can adapt their mechanisms to counteract the antagonistic effects of BCAs, thereby reducing the efficacy of these compounds over time. Studies suggest that repeated exposure to specific biological treatments can lead to adaptive resistance, where pathogens modify their metabolic pathways or develop protective biofilms to evade suppression [135]. Additionally, most applications of biological treatments are limited to preharvest stages. Thus, BCAs alone cannot mitigate pathogen risk during postharvest processes [136].

5 Plasma-activated Water

Plasma-activated water (PAW) is produced by subjecting water to non-thermal plasma generated at atmospheric pressure [137], [138], [139]. In particular, non-thermal plasma is a partially ionized gas containing reactive oxygen species (ROS) and reactive nitrogen species (RNS). When this plasma interacts with water, these reactive species are dissolved, creating a solution responsible for the antimicrobial effects of PAW [140]. In recent years, numerous studies have investigated the antimicrobial effectiveness of PAW. Rahman *et al*., highlighted PAW's broad-spectrum antibacterial activity, which is attributed to the presence of reactive oxygen and nitrogen species (RONS) [141]. Other articles have demonstrated PAW's potential in food safety and quality, showing significant microbial reduction in various food items [142], [143]. Moreover, a study by Miranda *et al*., using a coaxial dielectric barrier discharge plasma system, revealed the effectiveness of PAW against pathogens such as *Staphylococcus aureus* and *Escherichia coli* [144].

As shown in Figure 6, the commonly used systems for generating PAW include plasma jet, dielectric barrier discharge, and corona discharge. Additionally, there are also gliding arc discharges, as well as custom-built systems that have been developed and optimized for specific applications. Researchers customized the atmospheric pressure plasma jet by adjusting the settings like power, frequency, and gas mixture to achieve the desired PAW properties. In the study by Taaca *et al*., a custom-built atmospheric pressure plasma system was used to treat chitosan-acrylic acid (Cs-AA) blends. Despite operating at a low temperature of less than 40 °C, the system successfully generated RONS. Treatment time and gas flow rate were found to influence the pH and absorption spectrum of deionized water. Furthermore, the analysis revealed that varying gas flow rates affected the production of nitric oxide (NO) and hydroxyl (OH) radicals, while different discharge conditions influenced the concentrations of nitrogen (N) species [145]. These findings demonstrate the potential of custom-built plasma systems to produce PAW with specific properties.

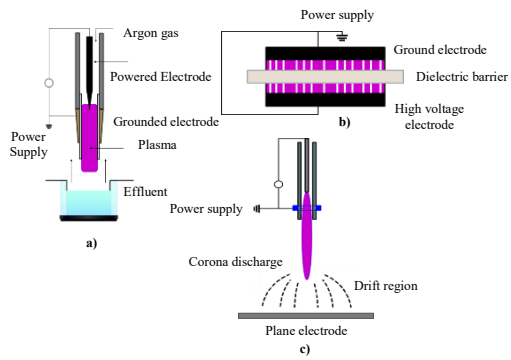

Figure 6: Systems in generating plasma-activated water; a) plasma-jet, b) di-electric barrier discharge, c) corona discharge.

5.1 *Physicochemical properties of PAW*

PAW is characterized by several chemical properties resulting from the presence of RONS. These properties significantly impact its effectiveness as an antimicrobial agent and its application across multiple fields. One of the most notable changes is the modulation of pH. Specifically, exposure to cold atmospheric plasma induces the formation of acids, such as nitric acid, resulting in a decrease in pH. This is accompanied by an increase in water activity (a_w), which is attributed to the presence of ions such as nitrate and nitrite. PAW also exhibits a higher oxidation-reduction potential compared to tap water, indicating its strong oxidizing properties.

Additionally, plasma activation reduces the surface tension of water, which enhances its applications as an antimicrobial agent [138], [146], [147]. Recent observations suggest that plasma activation significantly lowers the surface tension of water, indicating surfactant-like behavior. It also enhances PAW's ability to spread more efficiently on surfaces, improving its effectiveness in microbial inactivation and surface treatment applications. According to the study by Shaji *et al.,* the findings indicate that plasma activation decreases the surface tension of water and lowers the contact angle of droplets on glass surfaces at room temperature. The lower surface tension facilitates better penetration on surfaces for various applications. These changes suggest that plasma modifies the mesoscopic structure of water at lower temperatures. Moreover, it increases the viscosity of water at high temperatures, enabling better surface interaction and penetration. It also indicates an increase in a_w due to the presence of reactive species, such as hydrogen peroxide (H_2O_2), ozone (O_3), and nitrate ions (NO_3^-) [148].

5.2 *Pathogen inactivation mechanism of PAW*

The antimicrobial efficacy of PAW is primarily attributed to the presence of RONS, including hydrogen peroxide (H_2O_2), hydroxyl radicals (•OH), ozone (O_3), nitric oxide (NO), and peroxynitrite ($ONOO^-$). These reactive species disrupt microbial cells through oxidative stress mechanisms that damage key cellular structures and functions [144].

One of the primary modes of inactivation is membrane disruption. RONS can cause lipid peroxidation in microbial cell membranes, compromising membrane integrity and leading to cell leakage and death. Furthermore, oxidative damage to nucleic acids and proteins impairs microbial replication and enzyme function. Reactive species such as •OH and $ONOO^-$ can induce strand breaks in DNA and oxidize amino acid residues, denaturing critical microbial proteins [149].

PAW also interferes with biofilm formation and stability, a primary defense mechanism of many pathogenic fungi and bacteria. By penetrating and degrading the extracellular polymeric substances (EPS) matrix, PAW effectively destabilizes biofilms and increases microbial susceptibility to treatment [150]. In the study of Xia *et al*., researchers treated *Escherichia coli* and *Staphylococcus aureus* biofilms with PAW under controlled conditions to assess their impact on biofilm stability. Biofilms were cultivated on surfaces and exposed to PAW for varying durations, allowing researchers to observe changes in EPS and microbial viability. The findings demonstrated that PAW effectively disrupts biofilms by mechanically degrading the EPS matrix and directly targeting biofilm-associated cells in both gram-negative and gram-positive bacteria, leading to increased susceptibility to treatment [151].

The overall antimicrobial mechanism of PAW is multi-targeted and non-selective, making it difficult for pathogens to develop resistance. It makes PAW an up-and-coming alternative to chemical disinfectants, particularly for fresh produce like strawberries, where surface and internal contaminants pose a significant risk to food safety and shelf life.

6 Micro-Nano Bubbles

Micro-nano bubbles (MNBs) are tiny gas-filled bubbles generally in the range of micrometers and nanometers [9], [152]. As illustrated in Figure 7, bubbles with diameters ranging from 1 µm to 100 µm are referred to as microbubbles, while those with diameters of less than 1µm are called nanobubbles [153]. Specifically, bubbles in the range of 1 to 100 µm are typically used for bio-activity fields, those less than 100 µm for fluid physics fields, and analytical sciences require smaller than 1 µm. Aside from their small size, MNBs exhibit a substantial specific surface area, high zeta potential, prolonged stability in water, and enhanced oxygen transfer efficiency [154].

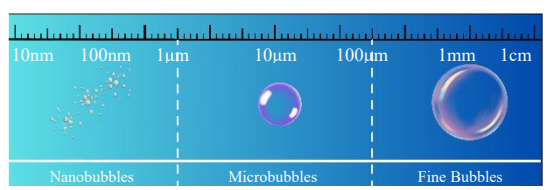

Figure 7: Schematic diagram of the size range of micro-nano bubbles.

MNBs have distinct physical properties that make them highly effective in various applications. Their small size allows them to remain suspended in liquids for extended periods without rising to the surface. This contributes to their prolonged stability, unlike larger-sized bubbles that quickly collapse. Additionally, MNBs exhibit high internal pressure, which increases as bubble size decreases, resulting in enhanced gas dissolution efficiency [153].

MNBs are continuously gaining attention in agriculture for their ability to help plant roots absorb nutrients more efficiently and improve soil aeration. Studies show that nanobubble-enriched irrigation water improves oxygen availability in the root zone, enhances plant growth, and increases crop yield. Notably, research on lettuce, tomatoes, and cucumbers demonstrates improved nitrogen use efficiency and increases in yield quality [155], [156]. MNBs can also be used in industries as a sterilizer and cleaning agent. Particularly, they contribute to pathogen inactivation through multiple mechanisms, primarily enhancing oxidative stress and disrupting microbial cell structures. Their high internal pressure facilitates the dissolution of ROS, such as hydroxyl radicals and hydrogen peroxide, which effectively degrade bacterial membranes and viral envelopes.

Additionally, MNBs generate physical shear forces that weaken biofilms, making pathogens more susceptible to antimicrobial agents. In the article by Ovissipour, the author examines their ability to remove biofilms and enhance cleaning efficiency [157]. In food science, researchers are investigating how MNBs can prolong the freshness of perishable foods, improve food texture, and enhance cleaning methods in food production. Research by Javed *et al*., explores the role of nanobubbles in food processing, examining their influence on food texture, extraction, freezing, and sanitation. It highlights their ability to improve mass transfer and stability in liquids [158].

6.1 *Generation principle of MNBs*

Micro-nano bubbles can be generated through various techniques, predominantly categorized into physical and chemical methods. Chemical techniques include electrolysis and chemical reactions, where gas is released into a liquid medium to form bubbles. Physical methods involve cavitation, gas dispersion, solution mixing, temperature alteration, and electrohydrodynamic (EHD) effects, all of which utilize fluid dynamics to produce stable micro-nano bubbles [159].

The stability of MNBs is a crucial factor in their production. Specifically, stability is influenced by factors like surface charge, gas solubility, and the presence of surfactants [160]. In particular, gas solubility also affects the persistence of bubbles. Gases with high solubility, such as carbon dioxide (CO_2), tend to dissipate more rapidly, whereas less soluble gases like oxygen (O_2) and nitrogen (N_2) can remain in liquid for more prolonged durations [161], [162]. MNBs exhibit unique properties, including slow buoyancy, negative surface charges, and increased mobility of water molecules, which contribute to their potential applications in various fields [163].

A fundamental principle governing bubble movement is Stokes' law, which states that a bubble's rising velocity is directly proportional to the square of its radius. Due to their small size, MNBs ascend at a negligible rate or may even remain suspended indefinitely, especially in viscous fluids [164]. Thermal energy in the liquid drives Brownian motion, continuously propelling bubbles into random motion and preventing them from rising conventionally. The high internal pressure, a consequence of the Laplace pressure being inversely proportional to the radius, compresses the gas inside each bubble, thereby improving gas dissolution efficiency through Henry's law [165], [166]. Their ability to remain active in solutions for longer than conventional gas bubbles underscores their significance in applications, particularly for pathogen inactivation.

6.2 *Pathogen inactivation mechanism of MNBs*

The application of MNBs in pathogen control spans various fields, including food safety, water treatment, and medical sterilization. The primary mechanisms of pathogen inactivation in MNBs involve the generation of reactive oxygen species (ROS) within the bubbles, which induce oxidative stress on microbial membranes, leading to lipid peroxidation and structural damage to the pathogen. Additionally, the high internal pressure and collapse dynamics of MNBs contribute to the disruption of biofilms, which further weakens the microbial defense mechanisms [11].

In oxidative damage, MNBs facilitate pathogen inactivation through enhanced gas solubility and diffusion. The small size and high surface area of these bubbles enhance the delivery of antimicrobial gases, such as ozone and hydrogen peroxide, increasing their efficacy against fungi and bacteria. A related study demonstrated that ozone micro-nano bubbles significantly improve disinfection capacity by prolonging ozone retention in water, thereby enhancing microbial inactivation. Furthermore, the interaction of MNBs with microbial cells can trigger changes in membrane permeability, leading to increased susceptibility to external stressors and antimicrobial agents [11]. Another study by Luo *et al*.,

investigated the impact of MNBs on biofilm growth within drinking water distribution systems. Researchers observed that MNBs significantly inhibited biofilm formation, particularly when combined with oxygen, leading to a 77.87% reduction in biofilm dry weight. The mechanism of MNBs' action varied across three phases of biofilm growth, including physical obstruction and chemical oxidation in the slow growth phase (0 to 27 days), oxidative inactivation in the rapid growth phase (27 to 42 days), and adsorption and scour in the dynamic stability phase (42 to 66 days). Specifically, MNBs initially form a hydrophobic layer on surfaces, making microbial adherence difficult. Their collapse generates hydroxyl radicals (•OH), which reduce bacterial numbers and favor the growth of oxidation-resistant bacteria. This method also decreased microbial diversity within the biofilm, with a 54.22 to 61.66% inactivation rate of planctomycetes and an 87.9% removal of total organic carbon (TOC) from the water [165].

Another research has shown that integrating MNBs with PAW and ultraviolet photolysis can significantly enhance microbial reduction in food products [167]. Furthermore, a study by Naewkanya and Petiraksakul investigated the effectiveness of carbon dioxide micro-nano bubbles (CO_2 MNBs), in combination with sodium hypochlorite (NaOCl) and sodium chloride (NaCl) solutions, for inactivating aerobic bacteria in tilapia fillets and extending their shelf life. The results showed that a specific combination of 100 mg/L NaOCl, 10% w/v NaCl, and 32 min of contact time with CO_2 MNBs significantly reduced the number of aerobic bacteria by 1.509 log CFU/g. Experimentally, this treatment achieved a reduction of 1.503 ± 0.009 log CFU/g, bringing the bacterial count down from 5.623 log CFU/g to 4.120 log CFU/g [168]. Moreover, Wang *et al*., reported that ozone MNBs significantly enhance the postharvest quality of spinach by preserving cellular integrity and slowing down senescence-related deterioration. By treating spinach with 4 mg/L ozone MNBs for 5 minutes and storing it at 20 °C for 8 days, the study demonstrated that ozone MNBs alleviate cell membrane damage, reduce malondialdehyde (MDA) accumulation, and maintain structural integrity. This treatment inhibits respiration and ethylene release, thereby delaying the loss of nutrients and oxidative damage. Also, it minimizes chlorophyll and vitamin C loss while promoting antioxidant enzyme activity, including peroxidase and catalase, which mitigate hydrogen peroxide accumulation [169]. However, these combined applications are limited only to exposure time and the type of pathogen. Thus, further optimization of treatment parameters is necessary to maximize their potential for food safety applications. It also highlights the need for further investigation into complementary control methods.

7 Comparative Analysis of PAW and MNBs as Pathogen Control Strategies

PAW exhibits strong antimicrobial properties due to the presence of RONS, while MNBs offer enhanced gas dissolution and prolonged bubble stability that aid in disrupting microbial cells. These two techniques differ in their modes of action. Particularly, PAW relies on chemically reactive species, whereas MNBs primarily use physical interactions. To further understand their potential, this section provides a comparative overview of PAW and MNBs as innovative approaches for controlling pathogens. By examining key parameters such as antimicrobial efficacy, cost-effectiveness, and operational limitations, Table 5 highlights the advantages and disadvantages of these methods as potential control measures for pathogens in strawberries.

Table 5: Efficacy, cost, and limitations of PAW and MNBs for pathogen control.

Pathogen Control	Generation Method	Efficacy	Cost	Limitations	Ref.
Plasma-activated water	Atmospheric pressure plasma jet	• Highly effective against a broad range of foodborne pathogens. • RONS can inactivate bacteria and disrupt biofilms • It shows good antimicrobial efficacy even at low frequency.	Moderate to High: Cost varies significantly with scale and specific system.	Efficacy can be influenced by factors such as feeding gases, discharge parameters, and initial microbial concentration.	[138], [141]

Table 5: (Continued).

Pathogen Control	Generation Method	Efficacy	Cost	Limitations	Ref.
	Di-electric barrier discharge	• RONS effectively inactivate *E. coli* and *Bacillus cereus*. • Suitable for treating sensitive biological materials due to the lower plasma temperature.	Low to High: The cost is dependent on scale and specific design.	It requires high voltage.	[138], [144], [170]
	Corona discharge	• RONS were produced. • Demonstrated efficacy in decontaminating food packaging films, with higher microbial inactivation under wet conditions.	Low to Moderate: Cost varies with electrode design and power source.	The discharge may eventually result in an arc discharge if the applied voltage surpasses the insulation resistance limit.	[171]
	Gliding arc discharge	• An effective plasma source for the activation of aqueous solutions. • Potential in microbial inactivation and wastewater treatment. • RONS were produced.	Low to Moderate: Cost varies with gas flow rate and system size.	Complex electrode design and potential ozone generation.	[148], [172], [173]
Plasma-activated water	Custom-built atmospheric pressure plasma system	• Demonstrated antimicrobial efficacy against spoilage bacteria on fresh produce and surfaces. • Performance depends on configuration.	Low to Moderate: Cost varies with design complexity and components.	Limited standardization and reproducibility in commercial settings.	[145], [174]
Micro-nano bubbles	Physical (air and water mixing)	Exhibit mass transfer efficiency, prolonged stability, and antimicrobial potential.	Low to Moderate: Cost varies in generator type and capacity.	High intensity forces may potentially damage surface structures in some applications.	[159], [175]
	Chemical (gas infusion)	• Enhances the delivery and reactivity of infused gases. • Enhanced bacterial inactivation.	Low to Moderate: Depending on gas source, equipment, and scale of operation.	Long term stability of the bubbles is influenced by the infused gas.	[159], [176]

8 Conclusions

Pathogen contamination in ready-to-eat fruits and vegetables, such as strawberries, remains a critical challenge in ensuring food safety, reducing postharvest losses, and maintaining consumer acceptance. Both fungal and bacterial pathogens contribute to rapid spoilage, reduced shelf life, and potential health risks, especially during postharvest handling. While conventional treatments are commonly used, they pose concerns related to chemical residues, environmental impact, and the risk of antimicrobial resistance.

Emerging technologies, such as PAW and MNBs, offer promising and sustainable alternatives. As part of the AOP, PAW generates RONS that effectively inactivate various pathogens. MNBs, on the other hand, enhance the delivery and stability of these reactive species due to their unique

physicochemical properties and potential to improve gas and water exchange at the cellular level.

Despite preliminary findings, the integration of PAW and MNBs for postharvest pathogen control in strawberries remains underexplored in scientific literature. Therefore, further analysis is necessary to comprehensively understand their synergistic mechanisms, optimize treatment conditions, and assess their long-term effects on fruit quality, nutritional value, and safety. Furthermore, additional research is needed to evaluate the effectiveness of combined PAW and MNBs treatment in actual storage environments, where fluctuating temperatures, humidity, and microbial diversity may impact efficacy. By understanding their impact on consumer safety and microbial resistance, this integrated approach holds great potential for advancing postharvest technologies, contributing to safer produce, reducing food waste, and promoting sustainable agricultural practices.

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Author Contributions

R.Q.: investigation, conceptualization, topic organization, writing an original draft, reviewing, and editing; J.S.: conceptualization, topic organization, reviewing, and editing. All authors have read and agreed to the published version of the manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

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