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Full Length Research Paper

A Study of Essential Oils' Anti-biofilm Modes of Action that Target Genes Related to Quorum Sensing, Motility, Adhesion, and Pathogenicity

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Food safety is greatly impacted by biofilms, which also result in significant financial losses. Essential oils (EOs), one of the innovative methods for managing biofilms, can be an eco-friendly strategy since they can influence both the early and mature stages of biofilm production. The anti-biofilm modes of action of essential oils (EOs) against five harmful bacterial species that are known to produce biofilms are described in this review. These strategies include disrupting the expression of genes linked to adhesion, pathogenicity, motility, and quorum sensing (QS). Because biofilms and QS are interdependent processes, EOs affect biofilm formation by interfering with the communication system (for example, by controlling the expression of the genes agrBDCA, luxR, luxS, and pqsA). Furthermore, QS is a crucial mechanism that controls the expression of genes linked to the pathogenicity, virulence, and survival of bacteria. Likewise, EOs affect how many virulence genes are expressed. Additionally, EOs work by altering the genes linked to bacterial adhesion and motility, such as those that produce curli (csg), fimbriae (fim, lpf), and flagella (fla, fli, flh, and mot), as well as the ica genes that synthesize polysaccharide intercellular adhesin by synthesis. For a deeper comprehension of the biofilm mechanisms of action of EOs, this review offers a thorough foundation on the subject.

Key words: Biofilm, Gene expression, Foodborne pathogens, Communication system, Green strategies, Natural agents.

INTRODUCTION

Food safety is greatly impacted by biofilms, which also result in significant financial losses. Essential oils (EOs), one of the innovative methods for managing biofilms, can be an eco-friendly strategy since they can influence both the early and mature stages of biofilm production. The anti-biofilm modes of action of essential oils (EOs) against five harmful bacterial species that are known to produce biofilms are described in this review. These strategies include disrupting the expression of genes linked to adhesion, pathogenicity, motility, and quorum sensing (QS). Because biofilms and QS are interdependent processes, EOs affect biofilm formation by interfering with the communication system (for example, by controlling the expression of the genes agrBDCA, luxR, luxS, and pqsA). Furthermore, QS is a crucial mechanism that controls the expression of genes linked to the pathogenicity, virulence, and survival of bacteria. Likewise, EOs affect how many virulence genes are expressed. Additionally, EOs work by altering the genes linked to bacterial adhesion and motility, such as those that produce curli (csg), fimbriae (fim, lpf), and flagella (fla, fli, flh, and mot), as well as the ica genes that synthesize polysaccharide intercellular adhesin by synthesis. For a deeper comprehension of the biofilm mechanisms of action of EOs, this review offers a thorough foundation on the subject.

In the early stages of biofilm formation, bacterial mobility is crucial, particularly for cell adhesion to a surface. The process of adhesion is facilitated by a variety of motility types, such as swimming, swarming, and twitching (Rossi et al., 2018).

Biofilms can survive harsh environments, improve structural integrity, and keep their cohesive structure thanks to the EPS matrix. Through diffusion-reaction inhibition, the EPS matrix can reduce the efficiency of antimicrobial drugs, leading to the development of tolerance, an uninherited feature (Flemming et al., 2016). The antimicrobials' bioactive ingredients can form complexes with the EPS, rendering them inactive. Additionally, using enzymes found in the biofilm matrix, EPS can break down antimicrobials (Goel et al., 2021). According to Lu et al. (2019), the biofilm matrix also shields microorganisms from environmental stressors such oxidizing chemicals, metals, desiccation, UV light, antibiotics, and the host's immune system. Biofilms are a major global concern for the food, environmental, and clinical industries because of these different reasons. Food items may become contaminated in the food business if biofilms are found on surfaces and tools used in food processing. If the bacteria linked to the biofilms are pathogens, this could have a major effect on health because they can result in foodborne disease cases or outbreaks (Rossi et al., 2022a). The enterohemorrhagic salmo-nella Around 200,000 confirmed instances of infection were caused by Escherichia coli and L. monocytogenes in Europe in 2022; these bacteria are known to form biofilms (EFSA, 2023). The food sector may become contaminated with Staphylococcus aureus, a bacteria that is known to cause food poisoning and severe skin and respiratory illnesses. This is mostly because of its capacity to create biofilms on equipment and the surfaces of both fresh and frozen meals that come from animals (Silva-de-Jesus et al., 2022). Additionally, because biofilms help the pathogen persist on surfaces used in food processing, Pseudomonas aeruginosa is frequently identified in a variety of vegetables, milk, and meat products (Nahar et al., 2021).

Numerous methods have been devised to manage biofilms. Sadly, the vast majority of chemical-based methods operate poorly or result in bacterial resistance. Due to their potent antibacterial properties, essential oils (EOs) may be a new biocontrol method. They are sometimes referred to as phytocomplexes since they are made up of many bioactive components. If the components are only found in trace levels, they can be classified as major compounds and secondary compounds. The interplay between the phytocomplex's different components produces its antibacterial activity. The type and concentration of chemical components, which establish the cellular targets, are the primary determinants of EOs' modes of action. Compared to antibiotics, which usually only include one chemical entity, bacteria find it more difficult to develop resistance against multicomponent EOs (Degirmenci and Erkurt, 2020). Actually, by focusing on different locations within microbial cells, EOs demonstrate strong antibacterial qualities. This mode of action reduces the emergence of drug-resistant strains by efficiently fighting germs without encouraging the development of resistance (D'Amato et al., 2024). The capacity of EOs to break down cellular structures, alter the fatty acid composition of the cell membrane, and disrupt the cytoplasmic membrane may be the reason for their antibacterial properties (Rao et al., 2019). Another potential mode of action would be the reduction of the proton motive force along with ATP depletion or ion and metabolite leakage, which would ultimately lead to cell death (Rao et al., 2019). Specifically, EOs have demonstrated exceptional effectiveness in preventing the formation of biofilms and eliminating them from a variety of surfaces (Rossi et al., 2022a). Microbial biofilms can be affected by EOs in a number of ways, including cell membrane rupture, QS activity blocking, bacterial motility inhibition, cell adhesion prevention, EPS production reduction, and cell proliferation suppression (Mahamud et al., 2022). Targeting the important genetic pathways found in biofilms is one of the ways that EOs regulate them. Thus, the purpose of this review is to clarify how EOs work against biofilms by modifying gene expression. To do this, genes involved in QS, virulence regulation, adhesion, motility, EPS control, and protein synthesis are selectively targeted. Proteomic, transcriptomic, and genetic methods have been employed to study how EOs reduce virulence and prevent biofilm formation. To understand the wide range of methods of action, this overview looks at some pathogenic bacterial species that are well-known for their ability to form biofilms, such as Salmonella enterica, Pseudomonas aeruginosa, Salmonella monocytogenes, Staphylococcus aureus, and Escherichia coli. Fig. 1 shows a schematic illustration of the main molecular targets of EOs in regulating the formation of biofilms.

2. Listeria monocytogenes

2.1. Genes regulation during biofilm formation in L. monocytogenes

Temperatures, pH levels, high salt concentrations, UV light, the presence of biocides, and heavy metals are just a few of the environmental stressors that L. monocytogenes, a foodborne pathogen, may adapt to, survive, and even develop in (Osek et al., 2022). The capacity of L. monocytogenes to build biofilms is a key component of its survival in the food processing environment. As a result, the virus spreads widely throughout food processing facilities and is able to withstand cleaning and sanitation measures (Rossi et al., 2022b).

Gene regulation during biofilm development is a very complex process. AgrBDCA, the SigB operon, and PrfA (Fig. 2) are the three systems that primarily regulate biofilm formation in L. monocytogenes (Finn et al., 2023; Zhang et al., 2020). The transmembrane protein AgrB in the Agr operon breaks down the precursor peptide AgrD to create signaling molecules called auto-inducing peptides (AIPs), which are then transported to the cell surface. However, the transduction signal system of bacterial cells is made up of the regulatory protein AgrA and the histidine kinase AgrC (Zhang et al., 2020). QS, which controls the genes encoding the adhesins necessary for biofilm formation, activates the system when the concentration of AIPs reaches a threshold (Gandra et al., 2019). Under adverse environmental conditions, the transcriptional regulators of SigB (or σB) are essential for maintaining L. monocytogenes homeostasis (Maggio et al., 2021). The PrfA system, the primary regulator of virulence factors, is synthesized by these regulators in concert with the Agr operon (Zhang et al., 2020). Actually, the pathophysiology of Listeria monocytogenes

depends on PrfA, the main regulator of Listeria pathogenicity island 1 (LIPI-1) (Mauder et al., 2006). The expression of several genes involved in the formation of L. monocytogenes biofilms can be directly regulated by PrfA. Furthermore, it can affect gene expression by interacting with other systems or regulons (Zhou et al., 2011). The primary QS-, virulence-, and stress-associated genes involved in surface attachment and biofilm formation in L. monocytogenes are encoded by the three regulatory systems that have been characterized (Avila-Novoa et al., 2023; Jiang et al., 2023; Poimenidou et al., 2023).

2.2. EOs and genes regulation in L. monocytogenes biofilms

The function of genes in L. monocytogenes surface attachment and biofilm formation has been clarified by a number of investigations (Avila-Novoa et al., 2023; Jiang et al., 2023; Poimenidou et al., 2023). Additionally, an increasing number of research have looked into gene regulation when EOs are present (Table 1). Marini et al. (2018) showed that Cannabis sativa L. EO significantly affected the motility of L. monocytogenes by downregulating the regulatory gene prfA and the motility genes flaA, motA, and motB. Furthermore, there was a considerable decrease in the pathogen's capacity to penetrate Caco-2 cells and create biofilms. Additionally, Upadhyay et al. (2012) looked into how the virulence factors of L. monocytogenes were affected by plant-derived antimicrobial chemicals such as trans-cinnamaldehyde, carvacrol, and thymol.

The three plant chemicals, according to the authors, dramatically reduced the expression of numerous pathogen virulence genes. Specifically, prfA, which codes for the virulence components motA and motB, is one of these genes. These elements are in charge of a portion of the flagellar motor, which helps bacteria move around. Adhesion protein transcription is also mediated by other genes. Furthermore, the chemicals suppressed the expression of genes including hly, which codes for the manufacture of listeriolysin O, intA and intB, which code for internalin, plcA and plcB, which produce phospholipase C, and actA, which codes for the ActA protein, which is implicated in host cell invasion and actin-based motility. According to Liu et al. (2021), thymoquinone, eugenol, and cinnamonaldehyde successfully suppressed the expression of genes linked to stress response and virulence in L. monocytogenes. Indeed, the suppression of the prfA and sigB genes was noted, indicating a connection to the pathogen's decreased capacity to form biofilms as indicated by the biofilm inhibition assay. According to dos Santos et al. (2023), the administration of 25 mg of piperine changed the transcription of the genes found in the L. monocytogenes prfA and the agr locus (agrA, agrB, agrC, and agrD). Additionally, the authors noted that the expression levels of the genes prfA, agrD, and agrB were up-regulated, indicating a defense mechanism against the effects of piperine on bacterial cell membranes, including oxidative stress, increased cell wall permeability, and membrane integrity loss (dos Santos et al., 2023). However, agrC was shown to be down-regulated, which may have altered QS and impeded the development and upkeep of biofilms (dos Santos et al., 2023). In this regard, Pieta et al. (2017) examined the differential transcriptome profile of L. monocytogenes in the presence of Baccharis psiadioides EO using RNA sequencing and reverse transcription quantitative polymerase chain reaction (RT-qPCR). They showed that virulence genes such actA, hly, and prfA were down-regulated while stress genes were up-regulated, indicating a decrease in the microorganism's ability to spread infection. Similarly, after exposure to Cymbopogon citratus EO, Hadjilouka et al. (2017) assessed the expression of genes linked to peptidoglycan production, fatty acid biosynthesis/metabolism, and virulence in strains of L. monocytogenes. The study discovered that all tested strains had down-regulated levels of the virulence genes hly and inlJ, which encode for virulence-associated internalin.

Adjusted There are multiple methods for blocking QS signals. molecules, such as signal binding, signaling molecule degradation, competitive inhibition, and genetic regulation systems (Liu et al., 2021). This information was modified from Nguyen et al. (2020). Regarding the latter, Guo et al. (2019) discovered by RNA-seq study that Citrus Changshan-huyou Y.B. Chang EO treatment caused a significant alteration in the QS pathway of L. monocytogenes. The QS pathway's genes were actually expressed differently. For example, agrA, agrB, and agrC were up-regulated while the signal peptidase-encoding genes spsB and sip were down-regulated. However, a recent study (Liu et al., 2021) found that treatment with sub-minimum inhibitory concentrations (sub-MICs) of cinnamaldehyde, eugenol, resveratrol, and thymoquinone enhanced the suppression of three QS-associated genes (agrA, agrC, and agrD), which in turn reduced the formation of biofilms in L. monocytogenes. Through the degradation of signal receptors or the release of signal-degrading enzymes and signal mimics, the authors hypothesized that the natural chemicals prevented the pathogen's Agr QS systems. Zhang et al. (2020) assessed the impact of Syzygium aromaticum EO treatment on the expression levels of the QS pathway in L. monocytogenes. According to the findings, the EO considerably decreased the relative expression levels of agrA, agrC, and agrD, which had an impact on L. monocytogenes' ability to build biofilms.

In conclusion, the study of natural substances has illuminated the varied capacity to influence different cellular pathways in L. monocytogenes, demonstrating a multidimensional strategy. These substances do, in fact, seriously impair the functions of virulence, QS, and motility. However, there is a dearth of information on the impact on metabolic functions and adhesion mechanisms (Table 1), most likely due to the absence of cellular features like curli or fimbriae that normally aid in attachment to inanimate surfaces in this pathogen. Additionally, the QS system regulates the formation of exopolymers, which is one of the components that facilitate adherence in L. monocytogenes.

3. Staphylococcus aureus

3.1. Sta. aureus gene regulation during biofilm formation

Staphylococcus aureus is A common foodborne pathogen in the food supply chain that contributes to issues with food safety is Staphylococcus aureus. Because it can form biofilms on food surfaces, food processing equipment, and water, St. aureus is a highly adaptable microbe that may live in a range of environments and cause food cross-contamination (X. Liu et al., 2023). Several extracellular matrix components, including as proteins, cellular debris, extracellular DNA (eDNA), and polysaccharide intercellular adhesin (PIA), are produced throughout the intricate process of St. aureus biofilm formation (DelMain et al., 2020). Poly-N-acetyl-β-(1–6)-glucosamine, or PIA, is the primary EPS component and is essential for bacterial cells to adhere to one another. According to Idrees et al. (2021), it exhibits a noteworthy role in colonization, biofilm development, illnesses linked to biofilms, and resistance to antibiotics. The icaR (regulatory) and icaADBC (biosynthetic) genes (Fig. 3) are products of the intercellular adhesion (ica) locus, which produces PIA (Xiao et al., 2024; Archer et al., 2011). Upstream of the ica operon, the icaR gene encodes a protein that, in the opposite transcription direction of the icaADBC genes, influences the synthesis of PIA in St. aureus. IcaA is a N-acetylglucosaminyl-transferase that uses UDP-N-acetylglucosamine as a substrate to create PIA oligomers. When IcaD is present, its effectiveness reaches a high degree of activity. Furthermore, IcaC contributes to the elon-gation of PIA generated by IcaAD. An enzyme called IcaB has PIA deacetylase activity, which gives PIA a positive net charge. This alteration causes the polymer to adhere strongly to the bacterial surface (Nguyen et al., 2020).

According to Campoccia et al. (2021) and Lister and Horswill (2014), eDNA may function as an electrostatic polymer that binds cells to a surface. When autolysins, which are encoded by the genes atlE, lytM, litH, litA, sle1, and lytN (Bao et al., 2015), and the murein hydrolase, which is controlled by the lrgA and cidA genes (Archer et al., 2011), cause cell lysis in St. aureus, eDNA is released. In particular, a murein hydrolase regulator that the cidA gene produces causes cell lysis during the creation of biofilms. Conversely, the lrg gene's up-regulation inhibits the production of biofilms, DNA release, and cell lysis. Additionally, a number of proteins, including the clumping factors A and B regulated by the clfA and clfB genes (Idrees et al., 2021) and the fibrinogen-binding proteins encoded by the fnbA and fnbB genes (Lister and Horswill, 2014), aid in bacterial attachment and the formation of the biofilm matrix. The Agr QS system and its positive regulator SarA are essentially the two primary biofilm regulators in St. aureus. Cell-to-cell communication is triggered by the secretion of an autoinducing protein (AIP), which activates the Agr QS system, which is made up of two gene pairs (agrA-agrC and agrB-agrD). The Agr system in St. aureus either governs the bacterial-host interaction at the infection site or regulates the development of several toxins and virulence factors (Idrees et al., 2021). Since both St. aureus and L. monocytogenes are Gram-positive, similarities between their Agr QS systems were noted. AgrD, AgrB, AgrC, and AgrA are the four proteins that are encoded by the genes that make up Gram-positive bacterial agr loci. Through Agr-mediated gene regulation, these proteins can regulate the synthesis of virulence factors and support cellular processes (Huang et al., 2022). The LuxS enzyme produces the interspecies autoinducer AI-2, which is also implicated in Sta aureus QS and interspecies cell communication, including the production of biofilms. By altering the transcriptional regulation of the ica locus in St. aureus, the LuxS/AI-2 system controls the production of biofilms (Guo et al., 2023). Notably, many Gram-positive and Gram-negative bacteria, including E. coli and St. aureus, have luxS homologues. This implies that the luxS system might function as a bacterial signaling system that is extensively dispersed.

Serine proteases (sspAB genes), staphylococcal cysteine protease operon (scpA), serine protease-like proteins (splA-F), thermostable nucleases (nuc), and other St. aureus virulence factors are regulated by the sarA gene, enabling biofilm development (Wu et al., 2021).

3.2. EOs and genes regulation in St. aureus biofilms

The material that is currently available emphasizes how EOs have multiple effects on the major regulators of St. aureus biofilms. The EOs and natural compounds mostly affect virulence and adhesion processes in relation to St. aureus, as indicated by Table 1. This is the case for cardamom, Cuminum cyminum, Cymbopogon flexuosus, linalool, Mela-leuca alternifolia, Satureja hortensis, and Valencia orange oil.

In fact, after treating St. aureus biofilm cells with Melaleuca alternifolia EO, Zhao et al. (2018) looked at the transcriptional profile of the cells to see if there were any changes in gene expression. The findings demonstrated that when the oil was treated with a sub-minimum biofilm inhibitory concentration, 304 genes displayed differential expression. The authors used real-time RT-PCR to confirm the expression alterations found by RNA-seq analysis. They found that the expression levels of sspA, lrgA, fnbB, and lytM were up-regulated, whereas those of sarA, icaR, and cidA were down-regulated. The researchers hypothesized that the oil's inhibitory mechanism might be related to the reduction in virulence factor production. Actually, a large number of St. aureus virulence genes, including some matrix adhesion genes, that appear to be involved in biofilm formation are influenced by sarA. Furthermore, they proposed that the EO affects eDNA release and PIA expression to influence the production of St. aureus biofilms. Actually, a murein hydrolase regulator that causes cell lysis during biofilm formation is encoded by the cidA gene. Furthermore, St. aureus produces PIA through the icaADBC operon, which suggests that biofilm inhibitors could target the ica genes.

It has been discovered that 0.12% linalool, one of the main ingredients of terpeneless cold-pressed Valencia orange oil, suppresses the expression of genes that produce biofilms in St. aureus, such as icaA, icaB, fnbB, clfA, clfB, and ebps. The main constituent of the extracellular matrix's elastic fiber, the elastin binding protein, is encoded by these genes (Federman et al., 2016; Kot et al., 2019). According to a recent study by Cui et al. (2020), St. aureus's expression of the icaR gene was up-regulated when exposed to cardamom EO. It was discovered that the icaR gene's protein prevented PIA production, which impacted biofilm formation.

Furthermore, at sub-MICs (0.625–1.25 µL/mL), Cuminum cyminum essential oil has demonstrated a noteworthy capacity to prevent biofilm formation in multidrug-resistant St. aureus. According to Wu et al. (2024), this was accomplished by significantly lowering the expression of the ICA and HLD genes by 2.33 and 3.13 fold, respectively. Citral, the bioactive ingredient in Cymbopogon flexuosus EO, also affected the signaling system and many metabolic pathways of St. aureus in a dual-species biofilm, according to a study by Gao et al. (2020). Specifically, treatment with 0.5% citral resulted in the down-regulation of AgrA and α-toxin (encoded by the hla gene), one of the pore-forming toxins that is crucial for cell-to-cell contacts and plays a significant role in the production of biofilms (Gowrishankar et al., 2016). Additionally, citral can cause the acpP, accA, and fapR genes—which encode essential elements for fatty acid biosynthesis—to be repressed (Gao et al., 2020). It's interesting to note that Zhao et al. (2018) found that the EO treatment significantly altered the levels of genes linked to the purine and pyrimidine metabolism pathways, amino acid biosynthesis pathways, and glycine, serine, and threonine metabolism pathways in St. aureus biofilm. In a different study, Sharifi et al. (2018) found that Satureja hortensis EO inhibited the formation of biofilms in St. aureus and that treatment with the EO's MIC/2 resulted in a significant down-regulation of the hld gene.

This gene is part of the QS cluster and controls the synthesis of virulence factors that are secreted, such as α-, β-, and δ-hemolysins (Qin et al., 2014). It also modifies the first step of cell adhesion (Salinas et al., 2022).

There doesn't appear to be much data on how natural substances impact St. aureus motility. Perhaps this is due to the fact that St. aureus has long been thought of as a non-motile bacterium, but its ability to move has only lately been discovered (Pollitt and Diggle, 2017). Specifically, there aren't many known types of motility in St. aureus. One is comet formation, which displays a number of observable characteristics associated with gliding motion. However, darting and spreading are two passive motilities. According to Pollitt and Diggle (2017), darting is movement controlled by surface transfer, whereas spreading is mass migration from a central colony.

4. Pseudomonas aeruginosa

4.1. Genes regulation during biofilm formation in P. aeruginosa

In patients with compromised immune systems, Pseudomonas aeruginosa is a nosocomial opportunistic bacteria that can cause severe acute and chronic infections. It can adapt to many settings and evade host immune defenses due to its exceptional genetic flexibility and several virulence factors (X. Li et al., 2023). The propensity of P. aeruginosa to create biofilms, which account for between 65 and 80 percent of nosocomial infections, makes it a highly significant species. This disease contaminates a variety of food groups, including water, milk, meat, fruits, and vegetables, even though it is primarily linked to hospital settings. Because of its great metabolic versatility, quick reproducibility, and capacity to adapt and proliferate at low temperatures, it is a significant contributor to food infections (Gao et al., 2023; X. Li et al., 2023). Among the various systems involved in P. aeruginosa biofilms, the QS system is the most intricate. In P. aeruginosa, the QS system controls the synthesis of several virulence factors and the creation of biofilms through the mediation of signal molecules (Brindhadevi et al., 2020). Las, Rhl, Pqs, and Iqs are the four main interconnected QS systems in Pseudomonas aeruginosa that are linked to the production of four distinct signal molecules (Fig. 4).

The Las system consists of LasR, a transcriptional regulator, and LasI, which catalyzes the synthesis of N-(3-oxododecanoyl)-homoserine lactone (PAI-1 or OdDHL). The transcriptional regulator RhlR and RhlI, which catalyze the production of N-butyryl-homoserine lactone (PAI-2 or BHL), are components of the Rhl system (Smith et al., 2002).

The second QS signaling system, which uses 2-heptyl-3-hydroxy-4(1H)-quinolone, sometimes referred to as the Pseudomonas quinolone signal (PQS), is connected to the two regulatory systems previously stated (Diggle et al., 2007). The pqsABCD operon is necessary for PQS synthesis, and PQS directly interacts with PqsR (García-Reyes et al., 2020), the operon's promoter region, and the PQS receptor to drive the expression of pqsABCDE. According to Coleman et al. (2008), the pqsA gene specifically codes for a predicted protein that is similar to acyl coenzyme A ligases and that activates anthranilate for entry into the PQS biosynthesis pathway, which involves the condensation of a fatty acid with anthranilic acid. Conversely, proteins involved in the synthesis of long-chain hydrocarbon compounds that condense with anthranilate are encoded by the pqsB, pqsC, and pqsD genes (Lin et al., 2018). 2-Heptyl-4-quinolone (HHQ), a precursor of signaling molecules, is synthesized under the guidance of the pqsABCD gene products (Diggle et al., 2006). In the biosynthesis of alkilquinolone signaling molecules, the pqsE gene functions as a thioesterase, hydrolyzing the biosynthetic intermediate to produce the HHQ (Drees and Fetzner, 2015). Nevertheless, it has been shown that pqsE has a role in the cellular response to PQS and in the production of virulence factors such pyocyanin, while not being necessary for PQS biosynthesis (Gallagher et al., 2002). It appears that PqsH hydroxylates HHQ to produce PQS. Remarkably, pqsH is regulated by RhlR and is not a component of the pqs operon (Bera et al., 2009). 2-(2-hydroxylphenyl)-thiazole-4-carbaldehyde (IQS), the fourth intercellular communication signal, belongs to a novel class of QS signal molecules. A cluster of non-ribosomal peptide synthase genes called ambBCDE is formed by the genes involved in IQS synthesis (Tuon et al., 2022).

4.3. EOs and genes regulation in P. aeruginosa biofilms

Numerous anti-QS substances, both synthetic and natural, have been studied against P. aeruginosa. Notably, it has been shown that treatments using EOs produced from various plants largely target P. aeruginosa's QS system (Table 1). Generally

speaking, a number of processes, including the interaction of oil constituents with the signal receptor, the suppression of signaling molecule production, and the degradation of signaling molecules, may be connected to the anti-QS activity of EOs (Rossi et al., 2022a).

Cinnamomum cassia bark essential oil and cinnamon aldehyde were found to suppress PQS production, swarming motility, and biofilm formation in studies examining P. aeruginosa QS. Thus, it was found that the down-regulation of QS systems contributed to the prevention of biofilm by cinnamonaldehyde (Kim et al., 2015). Based on their capacity to suppress AHL-dependent violacein synthesis and virulence factors such elastase, protease, pyocyanin, EPS generation, and biofilm formation in P. aeruginosa, Husain et al. (2015) found that Mentha piperita EO and menthol had QS inhibitory qualities. In a different study, Syzygium aromaticum bud oil changed the expression of the signaling systems-related P. aeruginosa pqsA gene, lowering gene transcription and influencing the QS signaling pathway by lowering kynurenine levels (Jayalekshmi et al., 2016). Furthermore, the authors showed that eugenol, the main ingredient in EO, interacts to the QS receptor by hydrogen bonding with the important amino acid residues of the LasR receptor (Arg61 and Tyr41) as well as hydrophobic interactions. According to Khan et al. (2023), Tagetes minuta EO strongly suppressed QS signals and the PQS system, interfering with the pqsA and pqsR genes and preventing P. aeruginosa from forming biofilms. Ocimum tenuiflorum extract was similarly found to have an anti-QS impact on P. aeruginosa because of its primary bioactive components, linalool and eugenol (Lahiri et al., 2021). The authors contended that the attenuation of the QS system (such as the Las, Rhl, and Pqs systems) through inhibition of the synthesis of the auto-inductors N-3-oxododecanyol-L-homeserine lactone, N-butanoyl-L-homeserine lactone, and 2-heptyl-3-hydroxy-4-quinolone was most likely how the QS inhibition was achieved. It has been demonstrated that geraniol, a cyclic monoterpene alcohol present in essential oils made from Cymbopogon martini, Monarda fistulosa, Aframomum citratum, and Thymus daenensis, has strong QS inhibitory activity against P. aeruginosa (Mączka et al., 2020). Geraniol reduced the expression of lasI, rhlI, and pqsABCDEH, which are responsible for PQS biosynthesis in the pqs system, according to W.R. Li et al. (2023). The expression of the genes lasR, rhlR, and pqsR, which code for three corresponding signal receptor proteins, was also suppressed by geraniol. Satureja khuzistanica EO suppressed the pathogen's pyocyanin synthesis and demonstrated eradication and inhibitory actions on P. aeruginosa biofilms (Ghaderi et al., 2021).

Apart from QS, Agastache rugosa, Cinnamomum cassia, cinnamon aldehyde, Mentha piperita, and Tagetes minuta were found to be efficient against cellular pathways such as meta- bolism, motility, and virulence (Table 1). Interestingly, it was shown that cinnamon bark oil inhibited the production of fimbriae by downregulating the expression of the gene csgAB, which is involved in curli formation. Furthermore, bis-(3′-5′)-cyclic dimeric guanosine monophosphate (c-di-GMP) production was decreased and P. aeruginosa pre-formed biofilms were dispersed by sub-MICs of cinnamonaldehyde (Topa et al., 2018). In many Gram-negative bacteria, this secondary messenger plays a crucial role in regulating the development of biofilms. It also controls the production of P. aeruginosa biofilms and is linked to the bacteria's transition from a motile to a sessile lifestyle (Ha and O'Toole, 2015).

5. Escherichia coli

5.1. Genes regulation during biofilm formation in E. coli

Although Escherichia coli is a frequent component of both human and animal microbiota, some strains can become foodborne pathogens due to the development of virulence characteristics. Food safety is seriously threatened by this (X. Liu et al., 2023). The food supply chains of fresh meat, fruit, vegetables, raw milk, and dairy products are affected because E. coli can form biofilms on both biotic and abiotic surfaces. In these food supply chains, the pathogen serves as a hygiene indication (Reg. EC No 2073/2005).

The life cycle of an E. coli biofilm includes intricate processes like adhesion, movement, and cell-to-cell communication that are also linked to virulence factors. Numerous elements are linked to E. coli surface attachment, cell-cell interactions, and microcolony formation, including extracellular polysaccharide, the QS system, curli fimbriae, type I fimbriae, Antigen 43, and colanic acid. Other bacteria, like the Gram-negative E. coli, also have PIA, which is linked to the production of biofilms by St. aureus. PIA and the ica locus are known as PGA and pgaABCD, respectively, in E. coli (Fig. 5). The poly-β-1,6-N-acetyl-D-glucosamine (PGA), one of the main exopolysaccharides of the E. coli biofilm matrix, actually plays a crucial role in biofilm formation by mediating cell-to-cell and cell-to-surface adhesion in biofilms (Sharma et al., 2016); the pgaABCD operon promotes the production of PGA (Lin et al., 2020). The luxS gene, one of the many QS systems in E. coli, is essential for regulating the gene expression of certain virulence factors, regulating motility, encouraging the production of biofilms, and affecting the architecture of biofilms (Sharma et al., 2016; Mayer et al., 2023). According to Walters and Sperandio (2006), LuxS is an enzyme that breaks down S-ribosyl-homocysteine into homocysteine and 4,5-dihydroxy-2,3-penta-nedione, a highly unstable substance that reacts with water and cyclizes to form a variety of furanones, including the precursor of autoinducer-2 (also known as AI-2). It is widely acknowledged that flagellar and curli gene regulation play a role in the transition of bacterial cells from the planktonic to the biofilm state (Besharova et al., 2016). The first cell-to-surface contact occurs in Salmonella spp. and E. coli when flagella, which are encoded by the fli and flh genes, function as a mechanism for active motility (Sharma et al., 2016; Hendriksen et al., 2021). The type I fimbriae, which are expressed by the fim genes, are a virulence factor in E. coli that plays a significant role in its attachment to surfaces, whereas the curli fimbriae, which are produced by the csg genes, bind to the extracellular matrix proteins (Sharma et al., 2016).

5.2. EOs and genes regulation in E. coli biofilms

The impact of EOs and their primary constituents on the expression of specific genes linked to E. coli biofilm formation has been the subject of numerous research articles in recent years. Carvacrol, cinnamon aldehyde, and eugenol are the primary chemical components found in Origanum spp., Cinnamomum spp., and Syzygium aromaticum essential oils (EOs), as shown in Table 1. Because these chemicals can target many cellular pathways at once, they have become important players in terms of their antibacterial and anti-biofilm effectiveness. Table 1 demonstrates how the chemicals and EOs work against E. coli by influencing the expression of genetic components involved in the manufacture of extracellular structures like flagella and fimbriae and mainly targeting pathways linked to adhesion and motility. This effect is most noticeable when trans-cinnamaldehyde, eugenol, and cinnamonomum cassia are used.

Using qRT-PCR, it was discovered that 0.01 percent (v/v) of Cinnamomum cassia bark oil dramatically reduced the expression of the csgA and csgB genes, which are implicated in the curli development of EHEC (Kim et al., 2015). The study showed that by lowering the synthesis of fimbriae, this EO prevents EHEC biofilm formation. Regarding the modulation of flagellar and curli genes, Kim et al. (2016) found that EOs from Pimenta racemosa, Syzygium aromaticum, and Pimenta officinalis at a concentration of 0.005% (v/v) prevented the production of around 75% of EHEC biofilms. Eugenol was the main constituent of the EOs, according to GC-MS analysis, indicating that it is primarily in charge of the anti-biofilm action. Indeed, it was discovered that eugenol inhibited the production of type I fimbriae genes (fimCDH), curli generating genes (csgABDFG), and ler and ler-controlled toxin genes. Additionally, clove EO inhibited the locus enterocyte effacement (LEE) transcriptional regulator ler gene as well as a number of adhesion and motility-related genes, including fimA, fimH, flhD, fliA, and motB. Additionally, carvacrol reduced or stopped the motility of E. coli O157:H7 by inhibiting the synthesis of flagellin (Burt et al., 2007). Furthermore, the expression of the fliC, fimA, and lpfA genes, which encode flagellin A, type I fimbriae, and long polar fimbriae, respectively, was reduced by carvacrol, eugenol, thymol, and trans-cinnamaldehyde (Baskaran et al., 2016). Recently, Lippia origanoides EO was discovered to adversely influence the expression of the fimH and pgaC genes in E. coli biofilms (Martínez et al., 2023). As a result, biofilm formation was inhibited, motility was lost, curli protein synthesis was impacted, and exopolysaccharide synthesis was disrupted.

The primary constituent of Agastache rugosa EO, (R)-(+)-pulegone, was found to down-regulate the expression of pgaABCD genes in E. coli in a different study by Gong et al. (2021). The study confirmed that pgaA was a possible and important target for pulegone in E. coli, but not just that. As a result, pga-mediated biofilm development and the other mediating pathways for biofilm formation were suppressed.

Several researchers have also looked into the EOs' ability to suppress E. coli QS. Indeed, carvacrol and the carvacrol chemotype's EOs from Origanum heracleoticum, Thymus daenensis, and Satureja hortensis seem to have an impact on QS (Table 1). In the study by Mith et al. (2015), enterohemorrhagic Escherichia coli O157:H7 (EHEC) treated with sub-MICs of carvacrol and Origanum heracleoticum EO exhibited a decrease in luxS gene transcription. The down-regulation of those linked virulence genes may have been influenced by this gene, which is widely known for its role in QS and in controlling the gene expression of certain virulence factors like ler and fliC. Sub-MICs of Thymus daenensis and Satureja hortensis essential oils significantly reduced the expression of luxS and pfs in EHEC, according to a recent study by Sharifi and Fasaei (2022). Furthermore, EHEC's ability to swim and swarm was adversely impacted by the QS system's restriction.

It has been demonstrated that EOs and their components target routes other than the main one responsible for anti-biofilm activity. Using MALDI-TOF-MS, Bołzik et al. (2018) examined the impact of EO components (guaiacol, α-pinene, carvacrol, thymol, cinnamaldehyde, citral, eugenol, geraniol, carvo-menthenol, carvone, and carene) on low-molecular-weight proteins from E. coli. Several variations in protein expression between the treated and untreated samples were noted by the scientists. A few of these alterations were found in 30S ribosomal proteins (S15, S19), DNA-binding protein (HU-alpha), a protein involved in biofilm formation (UPF0434), a typical stress response protein (YthA), and another that controls the synthesis of the erythromycin resistance protein (23S rRNA methylase leader peptide). The findings demonstrated the impact of EO chemicals on ribosomal function, antibiotic resistance, and biofilm development. EOs have an impact on the metabolic variables linked to E. coli's capacity to produce biofilms as well as the expression of virulence. Scotti et al.'s study from 2021 shown how Cymbopogon martini EO down-regulated the ompA. One of the main antigens in the outer membrane, OmpA, may help E. coli adhere to host cells by acting as a virulence factor.

In all studied pathogen strains cultivated in minimum media M9, C. martini EO suppressed ompA expression, suggesting that this gene is essential for biofilm formation. Furthermore, a factor linked to zinc homeostasis and biofilm production in zinc-deficient settings, the EO caused widespread suppression of the zinT and ykgM genes. It has been demonstrated that a number of negative effects, including the suppression of curli generation, bacterial adhesion, and biofilm development, arise when zinc homeostasis is disrupted (Lim et al., 2011).

6. Salmonella enterica

6.1. Genes regulation during biofilm formation in S. enterica

Like other pathogens, salmonella species can create biofilms on biotic and abiotic surfaces, including as glass, rubber, plastic, and stainless steel. They are linked to recurring hospital infections, particularly in patients with weakened immune systems (Guillín et al., 2021). Salmonellosis is also the most commonly reported zoonose, accounting for the greatest number of outbreaks and cases (EFSA, 2023). Many food processing companies, particularly in the poultry industry, have

isolated Salmonella strains with the capacity to form biofilms, which helps them persist in food processing environments and cause cross-contamination of food items (Pang et al., 2023). The QS system is one of numerous regulatory mechanisms that are linked to the control of biofilm formation in Salmonella species. Salmonella and E. coli employ distinct QS systems, including LuxR homolog SdiA/AI-1 and LuxS/AI-2 (Fig. 6). However, Salmonella spp. and E. coli cannot synthesize AHLs when the luxI gene is absent (Walters and Sperandio, 2006). Other bacterial species can sense QS signals through this receptor when they produce AHLs, however SdiA does not recognize an autoinducer made by Salmonella and E. coli (Walters and Sperandio, 2006; Styles et al., 2020; Jahan et al., 2022). However, S-adenosylhomocysteine (SAH) (Beeston and Surette, 2002; Mi et al., 2024) is necessary for bacterial cooperation as cell density rises (Kang et al., 2019), and the pfs gene product is necessary for the creation of AI-2. The Lsr transporter, an ATP-binding cassette transporter expressed by the lsr operon, is often responsible for returning AI-2 to the cell in Salmonella enterica. LsrK phosphorylates intracellular AI-2 (AI-2-P). The transcription of the lsr genes results from the binding of LsrR to AI-2-P, which in turn activates LsrR (Sholpan et al., 2021). On the other hand, LsrR suppresses both its own and the lsr operon's transcription in the absence of AI-2.

6.2. EOs and genes regulation in S. enterica biofilms

Many research have examined the antimicrobial and anti-biofilm properties of essential oils (EOs) against Salmonella species in recent years. Nevertheless, there is a paucity of research assessing how EOs affect gene expression. The several modes of action of the natural substances under investigation, each of which targets a distinct cellular component, are listed in Table 1. The QS system and its related pathways, including virulence, motility, adhesion, and metabolism, are significantly influenced by these mechanisms. Sub-MIC of Lippia origanoides EO reduced Salmonella enterica biofilm development in the Guillín et al. (2021) study, altering the expression of genes linked to QS and biofilm formation. Specifically, the expression of genes related to cell communication (sdiA, luxS, and luxR) and curli (csgA, csgB, and csgD) was suppressed. Additionally, there was a down-regulation of the motility genes (motB, flhD, and fliZ). Leesombun et al. (2023) recently discovered that Coleus amboinicus L. EO caused the down-regulation of genes linked to S. Typhimurium invasion (hilA), curli fimbriae formation (csgD), and motility (flhD, fljB, and fimD). According to a study by Hakimi Alni et al. (2020), the cellulose synthesis genes (csgD and adrA) and QS-related genes (sdiA and luxS) were down-regulated by MIC/2 of Allium sativum and Cuminum cyminum essential oils.

Syzygium aromaticum and Origanum vulgare are of special interest because of their exceptional capacity to alter the metabolic activity of S. enterica, thereby influencing a variety of pathways such as the tricar-boxylic acid cycle, oxidative phosphorylation, and fatty acid synthesis. Specifically, Y. Liu et al. (2023) found that genes linked to the metabolism of fatty acids (fadA, fadB, fadD, fadH, yafH,

In S. Derby biofilm cells treated with sub-MICs of Syzygium aromaticum (L.) and O. vulgare EOs, biofilm-formation was inhibited due to down-regulation of the TCA cycle (sdhD, sdhA, acnB, icaA, fumA, mdh, and lpdA), oxidative phosphorylation (cydA, cydB, frdA, cyoA, cyoB, cyoC, cyoD, cyoE, atpH, nuoC, nuoE, sdhA, sdhB, and sdhD), and TCA cycle (sdhE). Artemisia dracunculus EO also has an anti-QS action in Salmonella enterica (Mohammadi et al., 2021). Following treatment with MIC/2 of A. dracunculus EO, the authors noticed a considerable down-regulation of the pfs and luxS genes.

7. Conclusion

Because bacteria in a community lifestyle are resistant to external obstacles and can evade chemical treatments, biofilms pose a serious threat to the food industry and food environment.

Because of the increasing resistance linked to biofilms and the inefficiency of traditional anti-biofilm agents, scientific research has recently placed a greater emphasis on the antibacterial and anti-biofilm activity of natural agents. Numerous research looked into EOs' capacity to eliminate existing bacterial biofilms and stop new ones from forming. According to these results, EOs may be employed as substitute agents in the food business to fight biofilms. In actuality, a variety of cellular targets are impacted by the phytocomplex that makes up the EOs and its high level of molecular diversity.

Omics techniques like transcriptomics, genomics, and proteomics may be very helpful in pinpointing the precise targets (e.g. genes, proteins) in order to gain a better understanding of the anti-biofilm modes of action of EOs. Current research indicates that EOs' regulatory mechanisms against microbial biofilms are mostly caused by their inhibition of virulence factors, interference with the bacterial QS system, and their effects on motility, adhesion, EPS, and adhesion. Indeed, according to this research, EOs and their components disrupt the communication system by altering the expression of many genes, such as agrBDCA, luxR, luxS, sdiA, and pqsA, depending on the species under investigation. The expression of other virulence genes, including as prfA, hla, hld, hly, inlA, inlB, and inlJ, has also been found to be impacted by EOs. Furthermore, they suppress genes linked to bacterial adhesion and motilities, such as those that produce curli, fimbriae, and flagella.

Our analysis emphasizes that EOs and their constituents influence the expression of genes involved in biofilm formation not only at lethal concentrations but also at sub-MICs. This feature favors the use of EOs in the food industry, which has advantageous technological and economic ramifications. In actuality, the sensory perception and general acceptability of food products are positively impacted by the low concentrations of essential oils. Furthermore, it turns out that using EOs to control biofilms is profitable for food manufacturers.

The current study provides crucial information that will help researchers and the food industry improve the efficacy and

efficiency of EO treatments. The specifics of this information are as follows:

Combining what is now known about the processes by which EOs can inhibit and eliminate biofilms, with an emphasis on gene expression.

Allowing the bases to choose from a large range of EOs and their constituent parts in order to find those that can successfully prevent the development and destruction of biofilms.

By interfering with the pathways connected to particular genes, EOs have been shown to be able to block a number of bacterial pathogenic factors. These findings thus demonstrate that the use of EOs in the food business can prevent infections caused by ingesting bacteria as well as biofilms.

It is now essential for researchers and the food sector to employ green anti-biofilm tactics, like the usage of essential oils, and investigate their mechanisms of action in the current ecological transition phase.

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Declaration of competing interest

None.

Data availability

No data was used for the research described in the article.

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