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Exploiting endophytes to enhance aromatic and medicinal plant resistance to drought and salinity through the modulation of secondary metabolites and defense mechanisms

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Abstract

Background Aromatic and medicinal plants (AMPs) are more vulnerable to abiotic stresses such as drought and salinity, which contribute to a variety of biochemical, morphological, molecular, and physiological changes that impair plant growth and productivity. The use of symbiotic microorganisms is an approach to minimize the adverse effects of abiotic stressors on agriculture. Recently, interest in endophytic fungi and bacteria has grown because of the many benefits they provide to the host plant while reducing the use of chemicals in agriculture that benefit the environment and human health. The aim of this review is to summarize research on the use of bacterial and fungal endophytes to assist AMPs in combating drought and salinity, primarily through the modulation of secondary metabolites and defense mechanisms.

Methods A comprehensive literature review was conducted using the main scientific databases, including PubMed, ScienceDirect, Google Scholar, Scopus, and Web of Science, covering studies published between 2000 and 2025. The selection focused on experimental and review articles addressing the interaction between endophytic microorganisms and AMPs under abiotic stress. The data was analysed thematically to identify mechanisms of tolerance, plant-microbe interactions, and modulation of metabolic pathways.

Results Endophytes have proven their ability to protect plants, such as *Thymus vulgaris* L., *Rosmarinus officinalis* L., *Mentha piperita* L., and other plants, from abiotic stresses by directly or indirectly improving their immunity. Additionally, they enhance photosynthesis, improve plant growth, aid in nutrient mineralization, activation of antioxidant enzymes and produce bioactive compounds, hormones, enzymes, and volatile compounds, all of which improve plant productivity and stress resistance.

Conclusions Endophytic microorganisms represent a promising and eco-friendly strategy to enhance the resilience of AMPs against drought and salinity stress. By activating antioxidant defense systems, stimulating secondary

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metabolite biosynthesis, and improving physiological functions, these symbionts help plants maintain growth and productivity under adverse conditions. Their multifunctional role highlights their potential as sustainable biotechnological tools to reduce chemical inputs, promote environmental health, and support the development of climate-resilient agriculture. Future research should focus on field validation, molecular mechanisms, and the formulation of endophyte-based bioinoculants for large-scale agricultural applications.

Keywords Drought, Salinity, AMPs, Endophytes, Resistance

Introduction

Certain plants are classified as aromatic and medicinal plants because they possess significant therapeutic properties in addition to their nutritional value (Farhadi and Moghaddam 2023). Plant is considered medicinal if it has active compounds in one or more of its parts that have therapeutic properties. These plants are beneficial to human life because they are the source of modern medicines used to treat diseases, as well as being used for a wide range of other applications (Inoue and Craker 2014). Medicinal plants are considered a rich source of bioactive compounds such as alkaloids, terpenes, and phenols (Hussein and El-Anssary 2019), which can be used to the synthesis and development of drugs (Rasool Hassan 2012). In addition, they have demonstrated various pharmacological properties, including antiviral, anticancer, antibacterial, antifungal, and antiparasitic properties, as well as a strong ability to trap free radicals, thanks to the presence of vitamins, phenols, flavonoids, and anthocyanins (Chopra and Doiphode 2002).

According to Shao et al. (2008) plants are frequently subjected to a variety of environmental stressors that restrict their ability to grow and productivity as well as significantly reduce global agricultural output. Stresses from salinity and drought are persistent threats to agricultural crops worldwide and have been identified as the main barriers to increased productivity (Mahajan and Pal 2023).

Plants suffer from salt stress, which causes physiological and metabolic problems (Stefanakis et al. 2024), influencing the morphological traits, development, growth, yield, seed germination, survival rate, components, and quality of plants (Shao et al. 2008; Shtaya et al. 2021; Tarchoun et al. 2022). Salt stress generally reduces plant's rate of photosynthesis and respiration, but plants grown under salt stress have substantially higher levels of certain secondary plant products than plants grown under normal conditions (Said-Al Ahl and Omer 2011). Plant produces a variety of reactive oxygen species as a result of this abiotic stress (Siddiqui et al. 2017). Additionally, another major issue is drought, which limits the yield of aromatic and medicinal plants; the stress brought on by drought can hinder essential functions like respiration and photosynthesis, impacting different facets of plant metabolism and growth; medicinal plants respond to this stress by modifying their morphology and structure,

modifying genes that are resistant to drought, and increasing the production of secondary metabolites and osmotic regulators (Singh et al. 2018; Bistgani et al. 2024; Wang et al. 2024).

In light of the growing demand for aromatic and medicinal plants, strategies to increase agricultural productivity and reduce the hazardous impacts of various stress factors are necessary. The current review elucidated sustainable approaches, highlighting the potential use of endophytes as modern and innovative eco-friendly instruments for controlling and reducing stress in medicinal and aromatic plants. Endophytes are microorganisms (generally fungi and bacteria) that live inside the tissues of plants that are healthy without causing any symptoms of infection in their hosts (Wani et al. 2015).

Fungal endophytes have garnered more attention recently due to the many advantages they can provide to the plant host, either directly or indirectly, through the close relationship they form during plant tissue colonization (Young et al. 2013). Through a variety of mechanisms, such as the production of stress-related enzymes, promoting nutrient assimilation, osmolyte synthesis, activation of defensive systems in plants, and the modulation of plant hormone balance, endophytic fungi have demonstrated remarkable potential in mitigating the adverse consequences of drought and salt stress (Verma et al. 2022; Gowtham et al. 2024; Morales-Vargas et al. 2024; Ogbe et al. 2024). Moreover, they help increase photosynthesis rates, promote plant growth, aid in the mineralization of nutrients, and generate hormones, enzymes, and bioactive compounds, all of which enhance overall productivity and plant resistance to stress (Gowtham et al. 2024). As an illustration, thyme plants (*Thymus vulgaris*) inoculated with endophytic fungi (*Fusarium* sp., *Cladosporium puyae*, and *Cladosporium australiensis*) exhibited a significant increase in chlorophyll and carotenoids, as well as improved growth and significant antioxidant enzyme activity (SOD, CAT, POD, APX, and GR) compared to plants that were not inoculated under drought conditions (Kamyab et al. 2024a).

Apart from the connection between plants and endophytic fungi, the relationship between plants and endophytic bacteria has become a fascinating field of study that can be applied for novel agricultural practices (Ullah et al. 2019). Plant growth-promoting bacteria (PGPB) are among the best technologies for assisting plants in

withstanding challenging environmental conditions and enhancing plant growth through a number of processes, such as mineral uptake, phosphate solubilization, nitrogen fixation, phytohormone synthesis, and the generation of various volatile compounds (Ullah et al. 2019; Sharma et al. 2022; Hlongwane et al. 2023), and the generation of antioxidant enzymes like catalase, superoxide dismutase, and peroxidase, which provide protection against the harmful effects of reactive oxygen species (Gamalero and Glick 2022). For example, inoculation of *Arabidopsis* plants with *Priestia megaterium* significantly improved various growth parameters of the host plants under salt stress and drought conditions compared with those of non-inoculated plants (Hwang et al. 2022).

Abiotic stress is increasingly becoming a threat to plants, which is why the aim of our review is to highlight the importance of endophytes to improve plant adaptation to drought and salinity.

Biologically active compounds

Two words make up the term “bioactive”: “bio” means life, and “active” means dynamic or engaged in an activity (Bernard and Dromard 2011). It is also referred to as “biologically active” (Cammack 2006). For this reason, a bioactive substance is a compound that possesses a certain biological activity (Guaadaoui et al. 2014).

Bioactive substances can be distributed into essential and non-essential categories, wherein primary metabolites, compounds that are regularly produced and necessary for plant development and growth, are included in the category of essential compounds, and secondary metabolites, compounds that are typically not active in everyday situations but are generated in certain situations, are included in the category of non-essential compounds (Jamwal et al. 2023). Three broad families of secondary metabolites are phenolics, terpenes and alkaloids (Singh and Kumar 2023) (Fig. 1).

These bioactive substances can be derived from various natural sources, including microorganisms, plants, animals, and marine life (lichens) (Swamy and Akhtar 2019). Plants produce secondary metabolites in order to survive in their environment (Singh and Kumar 2023). These secondary metabolites are generally generated in response to abiotic and biotic stress factors, acting as protective agents against harsh conditions, herbivores, pathogens, and unfavorable environmental conditions (Divekar et al. 2022). They are essential for plant defense, signaling, and adaptability, as they act as antioxidants (phenolic, flavonoids, and stilbenes), antimicrobial agents (tannins, chitinases, and alkaloids), structural components (lignans and lignin), and growth regulators (terpenes and coumarins) (Liu et al. 2023).

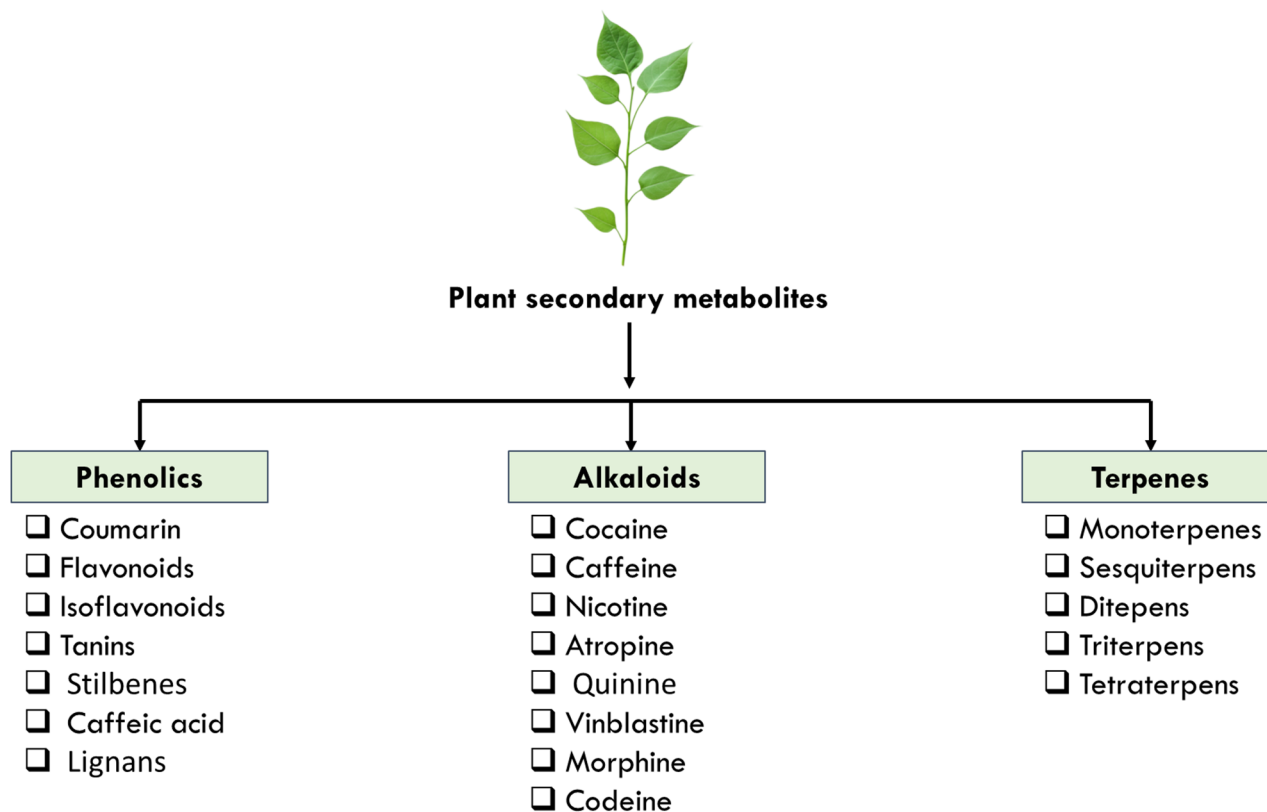


Fig. 1 Secondary metabolite classification

Terpenes play a crucial role in protecting plants against abiotic stresses such as salt and drought, which cause oxidative damage. As an illustration of the protective role of terpenes in saline environments, oleuropein aids plants in coping with oxidative stress brought on by elevated salt concentrations (Ahmad et al. 2022). Oleuropein acts as a glucose reservoir that facilitates osmoregulation and helps plants adapt to harsh saline conditions (El Yamani and Cordovilla 2024). Furthermore, terpenes are necessary for lowering oxidative stress, and stabilizing plant cell membranes (Khan et al. 2025). Some acidic terpenoids, such as zealexins and kauralexins, also function as phytoalexins, shielding plants from environmental stressors, including salinity and water deficit, as well as pathogens (Anjali et al. 2023). Additionally, certain terpenes, like carnosic acid, a diterpene, shield plants from drought stress and other environmental challenges (Khan et al. 2025). In order to protect plants from abiotic stressors, phenolic compounds are essential (Kumar et al. 2020a). Coumarins, a well-known class of phenolics, are present in plant membranes and are vital for plant defense (Kumar et al. 2020b). They act as antimicrobial and antioxidant agents, trapping reactive oxygen species (ROS) and preventing the growth of pathogens (Alshibl et al. 2020). Likewise, flavonoids are essential for abiotic stress responses such as salt and drought (Singh et al. 2024). Their antioxidant ability helps mitigate oxidative stress caused by environmental challenges (Shoaib et al. 2024). Flavonoids control stomatal behavior, improving water use in drought conditions by regulating the opening and closing of stomata, thereby increasing water use efficiency (Zhou et al. 2024). Collectively, these findings illustrate the multifaceted role of secondary metabolites in enhancing plant resilience to abiotic stress factors.

Influence of regulated environmental stressors on secondary metabolite production, growth suppression, and oxidative stress in aromatic and medicinal plants

Like other plant species, aromatic and medicinal plants face several constraints linked to weather conditions during their development and growth stages (Farhadi and Moghaddam 2023). Exposure to environmental and abiotic stresses like water scarcity, salinity, unusual temperatures, soil fertility, illumination, and carbon dioxide causes different physiological changes and alters the chemical composition of plants (Wang and Frei 2011). In addition, climatic conditions affect secondary metabolites (quantity and quality) as well as other items synthesized by medicinal plants (Mishra 2016). Secondary metabolism variations and the generation of active compounds in different qualities and quantities are crucial processes for plants in the face of adverse conditions (Zhang et al. 2017). The impacts of the environment on secondary metabolite synthesis and accumulation create

a complex network that, in addition to being species-specific, also differs within species (Moghaddam et al. 2020). Environmental factors can either increase or decrease the production of secondary metabolites by acting as abiotic stimuli on plant metabolism (Farhadi and Moghaddam 2023) (Tables 1 and 2).

Moreover, abiotic stress factors reduce the growth and productivity in several aromatic and medicinal plants such as *Rosa damascena* Mill. var. *trigintipetala* Dieck (Ali et al. 2014), *Pimpinella anisum* L. (Esim and Güneş 2021), and *Mentha canadensis* L. (Yu et al. 2015). According to Esim and Güneş (2021), applications of salt and drought were found to increase ROS such as H_2O_2 and O_2^- as well as lipid peroxidation while decreasing antioxidant enzyme activities like peroxidase and superoxide dismutase. Similarly, certain studies have shown that high salinity leads to an accumulation of malondialdehyde (MDA), considered a sign of lipid peroxidation (Kiarostami et al. 2010), leading to membrane degradation and, consequently, increased ion leakage (Ali et al. 2014; Hassan and Ali 2014). Abiotic stress factors induce oxidative stress through the overproduction of ROS in plants, which are involved in the damage of cell growth processes (Hajiboland and Joudmand 2009; Bernstein et al. 2010a, b). Plants detoxify ROS by trapping them, which is achieved by activating the antioxidant defense mechanism using antioxidant enzymes and non-enzymatic antioxidant components (Das and Roychoudhury 2014). The antioxidant enzymes include glutathione reductase (GR), dehydroascorbate reductase (MDHAR), guaiacol peroxidase (GPX), ascorbate peroxidase (APX), catalase (CAT), and superoxide dismutase (SOD) (Hassan et al. 2023). Non-enzymatic antioxidant components include flavonoids, carotenoids, α -tocopherol, glutathione (GSH), the osmolyte proline, and ascorbic acid (AA) (Mansour and Salama 2019; Hassan et al. 2023).

This review attempts to summarize the data concerning how the two main environmental factors, salinity and water deficiency, influence the regulation of secondary metabolite production, either promoting or inhibiting their accumulation.

Drought stress

One major issue is drought, which limits the productivity of medicinal and aromatic plants (MAPs). Stress caused by drought can disrupt essential functions such as respiration and photosynthesis, which can affect several aspects of plant growth and metabolism; to cope with these harsh conditions, medicinal plants resort to mechanisms like structural and morphological adjustments, modulation of drought-resistant genes, and increased synthesis of secondary metabolites and osmotic regulatory substances to mitigate stress (Bistgani et al. 2024; Wang et al. 2024; Zhang et al. 2025).

Table 1 Effects of drought stress on various aromatic and medicinal plants

S.No	Plant	Parameter effect	References
1	<i>Lavandula angustifolia</i> Mill	o Total protein and chlorophyll content decreased as water availability decreased, while control plants at 80% FC had the highest levels of flavonoids, phenolic compounds, and antioxidant activity.	(Hosseini and Heidari 2025)
2	<i>Silybum marianum</i> (L.) Gaertn	o In comparison to seeds from the control group (100% water capacity), silymarin and its components accumulated more when the water stress was severe.	(ElSayed et al. 2019)
3	<i>Hypericum brasiliense</i> Choisy	o Various phenolic compounds and betulinic acid showed increasing trends with increasing drought intensity.	(de Abreu and Mazzafera 2005)
4	<i>Mentha piperita</i> L.	o The amount of total phenol, flavonoid, and saponin is decreased. o Reduce the height and weight of the plant (fresh and dry weight). o The essential oil content is increased.	(Alhaithloul et al. 2019)
5	<i>Cucumis sativus</i> L.	o The cell membrane was stabilized by the higher activity and more robust expression of ROS-scavenging enzymes, SOD, CAT, APX, and soluble protein content. o Increased proline accumulation allowed cells to maintain their hydration status.	(Das et al. 2024)
6	<i>Rosmarinus officinalis</i> L.	o The percentage of essential oil is increased under light and moderate drought stress. o The quality of the essential oil is better under conditions of severe drought stress.	(Bidgoli 2018)
7	<i>Glycyrrhiza glabra</i> L.	o Induction of glycyrrhizine production in response to mild and moderate water stress. o Gradual decrease in biomass and relative water content of leaves. o Gradual increase in osmolyte concentrations (soluble sugars, glycine-betaine, and proline) in leaves and roots. o Induced oxidative stress (high levels of lipid peroxidation and hydrogen peroxide). o Increase in antioxidant enzyme activity.	(Hosseini et al. 2018)
8	<i>Labisia pumila</i> Benth	o Levels of anthocyanin and total flavonoids were induced. o Increase in anti-inflammatory and antioxidant response.	(Jaafar et al. 2012)
9	<i>Prunella vulgaris</i> L.	o High levels of ursolic acid and rosmarinic acid were observed under conditions of moderate drought stress.	(Chen et al. 2011)
10	<i>Catharanthus roseus</i> (L.) G. Don	o The amount of total phenol, flavonoid, and saponin is reduced. o Increased alkaloid content. o Reduce the height and weight of the plant (fresh and dry weight).	(Alhaithloul et al. 2019)
11	<i>Adonis amurensis</i> Regel & Radde and <i>Adonis pseudoamurensis</i> W. T. Wang	o Increased osmoregulant (proline), enzymatic activity (superoxide dismutase and ascorbate peroxidase), secondary metabolites (flavonoids, total phenols), and hormone concentrations (abscisic acid). o Lower H ₂ O ₂ content.	(Gao et al. 2020)
12	<i>Stellaria dichotoma</i> L. var. <i>lanceolata</i> Bge	o Moderate water stress promotes the production and accumulation of saponins. o Root biomass and secondary metabolites initially increased, then reduced as water stress levels rose.	(Zhang et al. 2017)
13	<i>Allium hirtifolium</i> Boiss	o With water stress, the concentration of allicin dialkylthiosulfinate increases.	(Ghassemi-Golezani et al. 2018)
14	<i>Camellia sinensis</i> (L.) Kuntze	o Increased antioxidant properties of plants under water deficit conditions	(Hernández et al. 2006)

In a series of experiments, it has been shown that plants subjected to water stress do indeed produce higher quantities of secondary metabolites (de Abreu and Mazzafera 2005; Selmar 2008; Hosseini et al. 2018; Alhaithloul et al. 2019). This concerns phenols and terpenes, as well as nitrogen-containing substances such as alkaloids, cyanogenetic glucosides or glucosinolates (Selmar 2008). It has been noted that although the content of active compound increases in response to drought, under extreme drought stress, the yield of these compounds does not always rise; it can also stay the same or even decline (Selmar 2008; Mahajan et al. 2020) (Fig. 2). It be noted that water deficit influenced secondary metabolism differs between and within species (Table 1),

depending on the stage of plant growth and the climate (Kleinwächter and Selmar 2015).

Salt stress

Salt stress is a major environmental obstacle that impairs the growth, development, and metabolic processes of MAPs. Salinity impairs vital physiological functions, including photosynthesis, water balance, and nutritional balance, while inducing oxidative stress; despite these constraints, MAPs exhibit notable physiological, biochemical, and molecular adaptation mechanisms, such as structural adjustments, antioxidant defenses, osmoprotectant biosynthesis, regulation of stress-responsive

Table 2 Impact of salt stress on various aromatic and medicinal plants

S.No	Plant	Parameter effect	References
1	<i>Silybum mari-anum</i> (L.) Gaertn	- o Salinity stress boosted the production of secondary metabolites, such as alkaloids, anthocyanins, and saponins. - o Impairing plant growth and development.	(Zahra et al. 2022)
2	<i>Rosmarinus officinalis</i> L.	- o An increase in rosemary's antioxidant activity and total phenolic content in salinity. - o Proline and malondialdehyde contents increased with salinity. - o Decreased photosynthetic pigment content.	(Kiarostami et al. 2010)
3	<i>Moringa oleifera</i> Lam	- o High salinity (100 mM) significantly decreased all growth parameters, which also resulted in an explosion of ROS as shown by elevated H₂O₂, MDA, and electrolyte leakage. - o Increased catalase and superoxide dismutase activity, with elevated levels of flavonoids, total phenols, glutathione, and ascorbic acid with strong capacities for decreasing power and radical scavenging.	(Azeem et al. 2023)
4	<i>Mentha pulegium</i> L.	- o Salt stress increases the essential oil content of this plant. - o Reduce plant growth.	(Aziz et al. 2008; Ghassemi-Golezani and Farhadi 2022)
5	<i>Stevia rebaudiana</i> Bertoni	- o Mild salt stress increased the diterpene content of this plant by up to 8.25%, but these compounds reduced by 4.2% under higher salinity intensity. - o Decrease in plant height, leaf fresh and dry weight. - o Decrease photosynthetic pigments. - o Increase in malondialdehyde content.	(Shahverdi et al. 2019)
6	<i>Plantago ovata</i> Forssk	o Saline conditions, whatever the level, increased the phenolic compounds of this plant.	(Verma and Shukla 2015)
7	<i>Fagopyrum esculentum</i> Moench	- o <i>F. esculentum</i> plants under salinity stress at a concentration of 75 mM had three times the amount of flavonoid rutin compared to plants that were not under stress. - o Accumulation of malondialdehyde, H₂O₂, osmolytes, and phenolic compounds increased with the intensification of salt stress. - o Increase in antioxidant enzyme activity. - o Reduction in seed yield and photosynthesis rate.	(Farhadi et al. 2022)
8	<i>Salvia macrocephala</i> Boiss	- o Under salt stress, the total phenol content of this plant was lower than that of unstressed plants. - o Impairs plant growth. - o Increase in the antioxidant content of the leaves.	(Valifard et al. 2017)
9	<i>Nigella arvensis</i> L.	o Salinity had a strong influence on phenol production and antioxidant activity in the seeds of this plant.	(Bourgou et al. 2009)
10	<i>Thymus vulgaris</i> L.	- o The increase in oil percentage was accompanied by a rise in salinity concentration. - o Decrease in plant height, fresh and dry mass.	(El-Din et al. 2009)
11	<i>Ocimum basilicum</i> L.	o Salt stress has led to an increase in the essential oil and carotenoid content of this plant.	(Bernstein et al. 2010a, b)
12	<i>Cucumis sativus</i> L.	- o The length of the roots was greatly reduced in all treatments. - o The amount of photosynthetic pigments was decreased. - o Proline, saponin content, and total antioxidant capacity were all decreased. - o Phenolic and flavonoid content increased. - o Some bioactive secondary metabolites were enhanced.	(Abdel-Farid et al. 2020)
13	<i>Lolium perenne</i> L.	- o Higher salinity reduced the length and dry weight of root and shoot. - o Chlorophyll <i>a</i>, <i>b</i>, and carotenoid contents dramatically dropped across all saline treatments when compared to the control. - o Similarly, in saline treatments, glutathione and malondialdehyde contents increased while superoxide dismutase and peroxidase activities decreased.	(Xu et al. 2020)
14	<i>Alcea rosea</i> L.	- o Increase secondary metabolite production. - o Some varieties had higher levels of total flavonoid and phenolic content, while others had lower levels.	(Sadeghi et al. 2024)

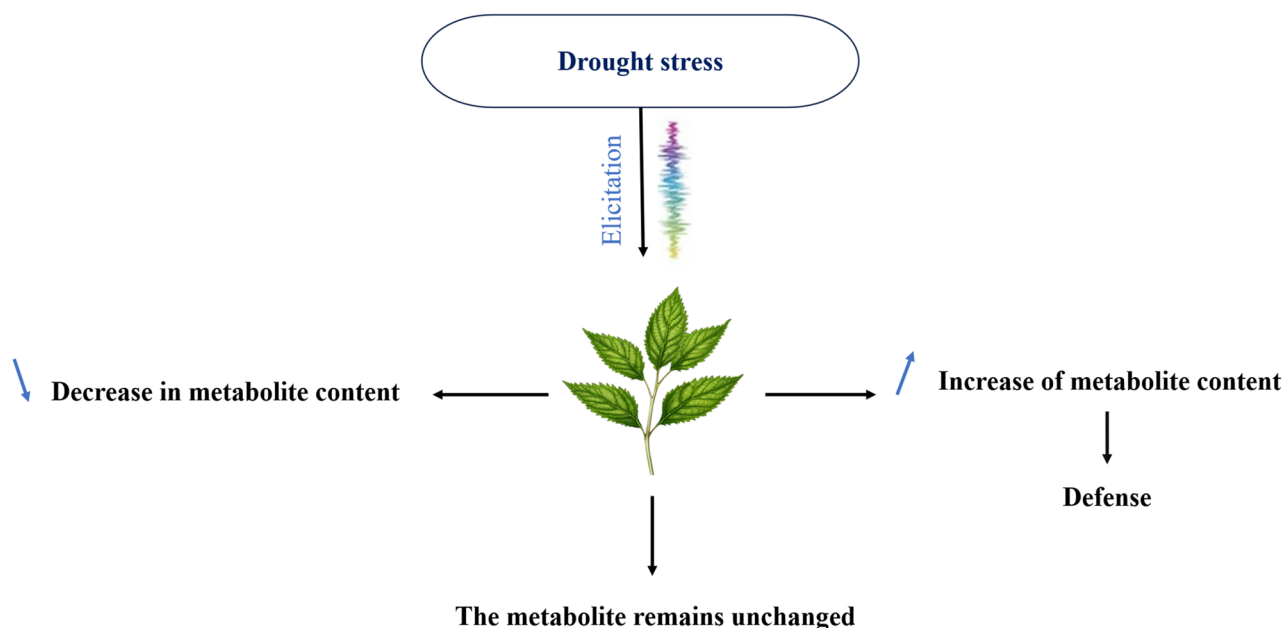


Fig. 2 Impact of drought stress on secondary metabolite production in aromatic and medicinal plants

genes, and production of specialized metabolites (Balasubramaniam et al. 2023; Ahmadi 2025).

Salt stress has a major impact on the biosynthesis of various active compounds in medicinal plants (Farhadi and Moghaddam 2023) (Table 2). Sytar et al. (2018) state that plants under stress frequently accumulate secondary metabolites, including different elicitors or signal molecules.

Role of endophytes in enhancing medicinal plant resistance to abiotic stress through secondary metabolites production

Like other plant groups, medicinal plants are constantly subjected to abiotic stress; however, they typically manage to survive by a variety of evolved strategies, such as secondary metabolite production (Yang et al. 2018).

Abiotic stressors like dryness, salinity, heat stress, and oxidative stress are interconnected, resulting in the production of ROS, which damage cells and ultimately lead to their death when exposed for prolonged periods (Wang et al. 2003; Waqas et al. 2012).

According to Ludwig-Müller (2015), important changes in symbiotic secondary metabolism occur during plant-endophyte interactions, and these changes may be caused by (a) the host inducing endophyte metabolism, (b) inducing host metabolism by the endophyte, (c) some metabolic pathways are partially shared by the endophyte and host, (d) the endophyte possibly metabolizing secondary host compounds, or (e) the host metabolizing endophyte products. It has been reported that plants and endophytes' relationship play a crucial role in enhancing medicinal plants' tolerance to abiotic stress by promoting

the buildup of antioxidants (Ogbe et al. 2020). Endophyte-colonized plants are frequently healthier and less vulnerable to the negative consequences of abiotic stress than their uninfected counterparts (Waller et al. 2005; Saikkonen et al. 2010). Several studies have shown that endophytes support medicinal plants in stress management by promoting the generation of secondary metabolites with antioxidant properties (Wang et al. 2025). For example, inoculation with endophytes derived from Lamiaceae induced drought tolerance in aromatic and medicinal plants such as thyme (*Thymus vulgaris*) and *Endostemon obtusifolius*, resulting in improved growth, increased accumulation of secondary metabolites, and increased antioxidant activity under stress conditions (Ogbe et al. 2024; Kamyab et al. 2024a).

However, some of this research has been conducted on model or cultivated plants, and there are few studies that focus specifically on plants with medicinal properties. Currently, studies establishing a direct link between the production of secondary metabolites attributed to endophytes and increased resistance to abiotic stress in medicinal plants are still rare, highlighting the importance of more specific research.

Fungal endophytes contribution to abiotic stress mitigation

Research has shown that inoculating plants with fungal endophytes increases their resistance to drought by improving their root biomass, total biomass, stomatal conductance, pigments, photosynthesis, transpiration, nutrient content, leaf morphology and anatomical structure, and antioxidant enzyme activities, and this is

because the link between plants and symbionts is positive (González-Teuber et al. 2018; Liu and Wei 2021) (Fig. 3). Additionally, fungal endophytes enhance plant salt tolerance by regulating endogenous hormones, modifying defense gene expression, and the antioxidant system, which contribute to lowering the ROS concentration (Siddiqui et al. 2022; Lubna et al. 2022) (Fig. 3). The mutualistic interaction of phytohormone secreting endophytic fungi can facilitate the growth of plants and mitigate the adverse effects of salt stress by regulating endogenous phytohormones, accumulating proline and antioxidants, protecting roots from absorbing salt by establishing a physical barrier, and maintaining ionic homeostasis and plant water potential (Khan et al. 2012; Ali et al. 2022).

Endophytic fungi can provide plants with a fitness advantage in situations where water is scarce (Abo Nauh et al. 2021). The increased drought tolerance of perennial ryegrass and tall fescue as a result of infection with the endophyte *Neotyphodium coenophialum* is arguably the most well-documented example of drought stress tolerance in plants mediated by endophytes (Dastogeer and Wylie 2017). Some fungal endophytes can give plants the ability to withstand drought, regardless of their natural habitat (Rodriguez et al. 2008). Furthermore, Rodriguez et al. (2008) discovered that salt-sensitive plants, which typically do not thrive in coastal environments, could acquire salt tolerance when inoculated with the endophyte *Fusarium culmorum*.

At least two processes are involved in symbiotically conferred abiotic stress tolerance: (1) the host's stress response systems are activated quickly after stress exposure, enabling the plants to prevent or lessen the effects of the stress (Redman et al. 1999) and (2) biosynthesis of biochemical substances with anti-stress properties by endophyte (Schulz et al. 2002).

Table 3 shows how fungal endophytes assist plants in their tolerance of salt and water stress.

Endophytic bacteria contribution to abiotic stress mitigation

As well as inoculating plants with fungal endophytes to lessen the impact of abiotic stress, endophytic bacteria also play a crucial part in plants' ability to resist abiotic stress, particularly drought and salinity. According to recent research, PGPB use a variety of strategies to increase a plant's capacity to withstand drought and salt stress (Gepstein and Glick 2013; del Carmen Orozco-Mosqueda et al. 2020; Gamalero and Glick 2022). These mechanisms include the fixation of nitrogen (Iniguez et al. 2004), phosphate solubilization (Lee et al. 2004; Ullah et al. 2017) and the synthesis of auxins, particularly indoleacetic acid, which directly stimulates the growth of plants; synthesis of antioxidant enzymes like peroxidase, catalase, and superoxide dismutase, which stop ROS harmful effects (Gamalero and Glick 2022) (Fig. 3). In addition, endophytic bacteria release a variety of compounds, such as plant growth regulators, at very low

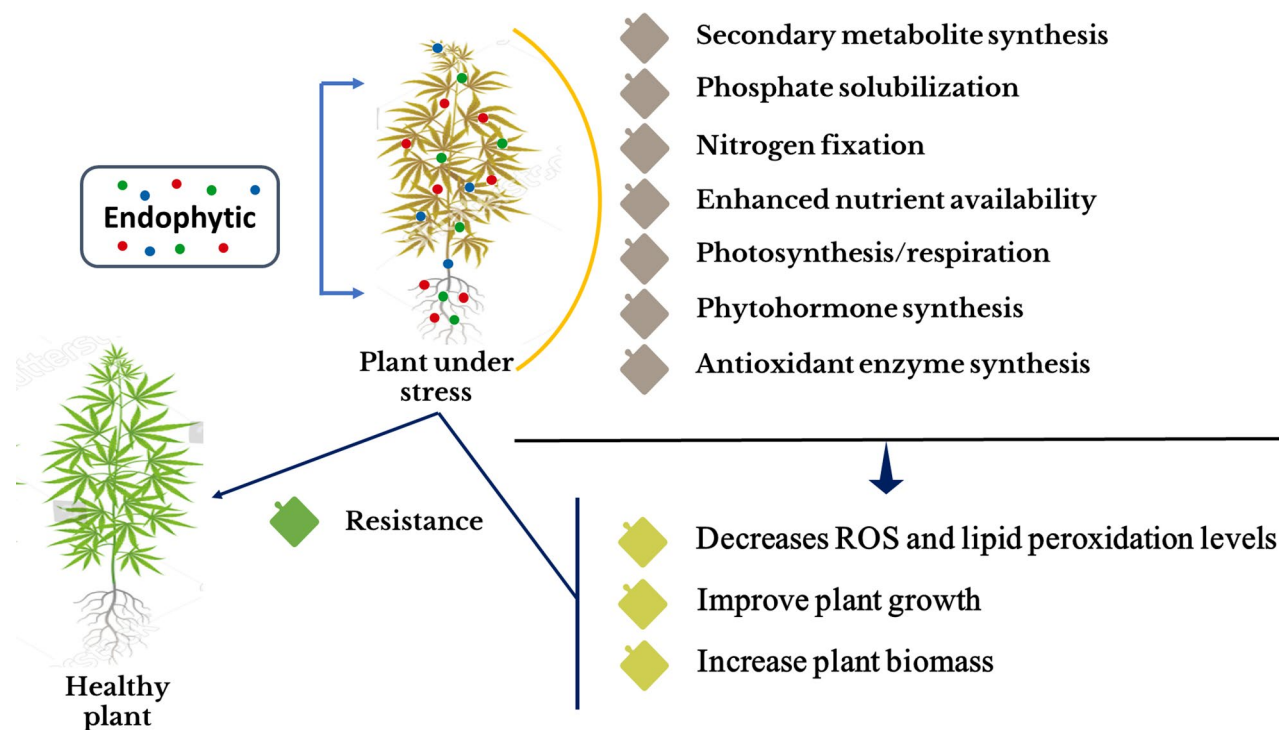


Fig. 3 Role of endophytes in mitigating abiotic stress

Table 3 Endophytic fungi mediated tolerance to salt and drought stress in aromatic and medicinal plants

Endophytic Fungi	Host plant	Stress	Major effects	Reference
<i>Penicillium citrinum</i> , <i>Dothideomycetes spp.</i> , and <i>Aurobassium pulluntis</i>	<i>Citrus reticulata</i> L.	Drought	o Reduce the activities of monodehydroascorbate reductase, CAT, and dehydro- ascorbate reductase while increasing the activities of SOD, GR, APX, and levels of GSH and ASA.	(Sadeghi et al. 2020)
<i>Penicillium chrysogenum</i> , <i>Penicillium brevicompactum</i> ,	<i>Lactuca sativa</i>	Drought	o Reduce root biomass and lipid peroxidation while proline content, shoot biomass, and total biomass are all rising.	(Molina-Montenegro et al. 2016)
<i>Fusarium sp.</i> , <i>Cladosporium puyae</i> , and <i>Cladosporium australiensis</i>	<i>Thymus vulgaris</i>	Drought	o Improve drought tolerance in <i>T. vulgaris</i> . o Improve plant growth parameters. o Reduce lipid peroxidation levels. o Higher antioxidant enzyme activity.	(Kamyab et al. 2024a)
<i>Aspergillus fumigatus</i>	<i>Oryza sativa</i>	Drought	o Increase in capacity antioxidants in vitro and in vivo.	(Qin et al. 2019)
<i>Penicillium resedanum</i>	<i>Capsicum annuum</i>	Drought	o Increase shoot length, CAT, GR, POD, SA, and chlorophyll content while decreasing EC and MDA.	(Khan et al. 2013)
<i>Fusarium oxysporum</i>	<i>Endostemon obtusifolius</i>	Drought	o Improvement of growth and stress tolerance mechanisms. o increased production of osmolytes (proline, soluble sugars). o Increased regulation of the antioxidant enzyme system (superoxide dismutase). o Higher concentration of antioxidant metabolites (flavonoids, phenols totaux). o Improvement of the osmoregulatory network, biochemical responses, and therapeutic efficacy of <i>E. obtusifolius</i> .	(Ogbe et al. 2024)
<i>Piriformospora indica</i>	<i>Hordeum vulgare</i>	Drought	o Colonized and boosted the biomass of the plant, as well as accumulated proteins participant in photosynthesis, signal transduction, ROS scavenging, and plant defense responses.	(Ghabooli et al. 2013)
<i>Fusarium acuminatum</i> , <i>Paraboeremia putaminum</i> , and <i>Acrocalymma vagum</i>	<i>Glycyrrhiza uralensis</i>	Drought	o Increases biomass, glycyrrhizin content, and glycyrrhizic acid. o Improve root development and nutrient absorption. o Beneficial effects on physiological and morphological parameters. o Enhanced antioxidant activity.	(He et al. 2019)
<i>Microdochium majus</i> , <i>Meyerozyma guilliermondii</i> and <i>Aspergillus aculeatus</i>	<i>Moringa oleifera</i>	Drought	o Improved primary and secondary metabolites, total chlorophyll, carotenoids, and plant growth characteristics. o Decreased levels of abscisic acid. o Enhanced activity of APX and CAT, two antioxidant enzymes. o Lowered production of ROS.	(Javed et al. 2022)
<i>Aspergillus oryzae</i>	<i>Thymus vulgaris</i> L.	Drought	o Improve the production of phenolic compounds, and flavonoids. o Higher levels of coumaric acid. o Increase the percentage of essential oil	(Kamyab et al. 2024b)
<i>Piriformospora indica</i> and arbuscular mycorrhiza	<i>Mentha piperita</i> L.	Salt	o Enhanced the ability of this plant to mitigate the adverse effects of the salt stress. o Increase in essential oil content and the antioxidant ability.	(Khalvandi et al. 2021)
<i>P. macrospinosa</i> , <i>N. goegapense</i> , and <i>N. chichastianum</i>	<i>Hordeum vulgare</i> L.	Salt	o Several physiological and biochemical indicators, such as proline, antioxidant enzyme activity, chlorophyll concentrations, and plant growth parameters, increased.	(Hosseyini Moghaddam et al. 2022)
arbuscular mycorrhiza fungi (AMF) and <i>Trichoderma koningii</i>	<i>Ocimum basilicum</i> L.	Salt	o Promotes plant growth (number and leaf area). o Accumulation of phenolic acids (caffeic, rosmarinic, ferulic, and chicoric). o maintenance of photosynthesis.	(Saia et al. 2021)
<i>Stemphylium lycopersici</i>	<i>Zea mays</i>	Salt	o Reduced levels of malondialdehyde, increased levels of phenolics and flavonoids, indole acetic acid, and antioxidant enzyme activity (APX and CAT).	(Ali et al. 2022)
<i>Piriformospora indica</i>	<i>Aloe vera</i> L.	Salt	o Increased levels of flavonoids, flavonols, phenol, and aloin, as well as radical scavenging activity at all salinity levels. o Increase in photosynthetic pigment content. o Overall rise in plant biomass, as well as an increase in the number of shoots and roots and their length.	(Sharma et al. 2017)
<i>Fusarium clavum</i>	<i>Cucumis melo</i>	Salt	o Demonstrated activities that promote plant growth, such as the solubilization of phosphate, production of indole acetic acid, and hydrolytic enzymes. o Enhanced plant weight, height, and number of leaves; transpiration; photosynthesis; stomatal conductance; and membrane stability. o Enhanced levels of phenolic content, GPX, CAT, SOD, and chlorophyll. o Elevated proline accumulation. o Reduced lipid peroxidation, along with lower levels of hydrogen peroxide, superoxide ion production, and cell death.	(Meshram et al. 2023)

Table 4 Endophytic bacteria mediated tolerance to salt and drought stress in aromatic and medicinal plants

Endophytic bacteria	Host plant	Stress	Role of endophytes in the host plant (Major effects)	References
<i>Pseudomonas pseudoalcaligenes</i> and <i>Pseudomonas aeruginosa</i>	<i>Hyptis suaveolens</i>		- Improves plant growth, but inoculation with endophytic bacteria leads to a drop in essential oil content and yield; however, due to improved vegetative growth, overall yield increases. - Reduces the phenolic content when under stress and raises it under normal conditions	(Jha 2019)
<i>Pseudomonas</i> sp.	<i>Glycine max. L</i>	Salt	- Encourages plant growth and stimulates the appearance of soybean seeds in the presence of salt stress. - Generates indole-3-acetic acid when salt stress is present.	(Kasotia et al. 2012)
<i>Azospirillum brasilense</i>	<i>Phaseolus vulgaris</i>	Salt	- Encouraged root branching - Rise the secretion of flavonoids that induce nodulation genes.	(Dardanelli et al. 2008)
<i>Streptomyces</i> sp.	<i>Oryza sativa L</i>	Salt	Improved water content, chlorophyll, proline, K⁺, Ca²⁺, and plant growth, while ethylene and ROS were reduced.	(Jaemsaeng et al. 2018)
<i>Chaetomium globosum</i>	<i>Moringa oleifera</i>	Salt	Increase the germination percentage and survival rate, biomass characteristics, K, P, N and total chlorophyll in moringa leaves under saline conditions.	(Soliman et al. 2022)
<i>Bacillus subtilis</i>	<i>Cicer arietinum</i>	Salt	- Decreased ROS and lipid peroxidation in stressed plants. - Increased plant biomass and photosynthetic pigment synthesis. - During bacterial association, stressed plants showed increased levels of glutathione and ascorbic acid, the total phenol content, and the activities of ROS scavenging antioxidant enzymes.	(Abd_Allah et al. 2018)
<i>Azospirillum lipoferum</i>	<i>Thymus vulgaris L.</i>	Drought	- Increase in fresh and dry biomass. - Increase in antioxidant enzyme activity (PAL and PPO). - Improve total phenol production and phenolic acid (ferulic, caffeic). - Improve the quality of essential oil.	(Kamyab et al. 2024b)
<i>Paenibacillus polymyxa</i>	<i>Endostemon obtusifolius</i>	Drought	- Improvement of growth and stress tolerance mechanisms. - Increased levels of antioxidant metabolites, such as flavonoids and total phenols. - Improvement of the osmoregulatory network, biochemical responses, and therapeutic efficacy of <i>E. obtusifolius</i>. - Enhanced regulation of superoxide dismutase, an antioxidant enzyme system. - Increased production of osmolytes (proline, soluble sugars).	(Ogbe et al. 2024)
<i>Pseudomonas fluorescens</i> WCS417 r and <i>Bacillus amylobacteriens</i> GB03	<i>Mentha piperita</i>	Drought	- Plants inoculated with PGPR exhibited a reduction in the adverse effects of drought. - significantly higher total phenolic content. - Higher enzymatic activities. - Inoculation decreased proline levels. - Reduce membrane lipid peroxidation.	(Chiappero et al. 2019)
<i>Mitsuraria</i> sp. ADR17 and <i>Burkholderia</i> sp. ADR10	<i>Zea mays</i>	Drought	Decreased evapotranspiration and altered the levels of proline and malondialdehyde in plants, as well as the antioxidant enzymes' activity and phytohormones under water stress.	(Huang et al. 2017)
<i>Pseudomonas fluorescence</i>	<i>Ocimum gratissimum</i>	Drought	- Enhanced growth of clove basil. - Increased essential oil constituents. - Improve basil's resistance to drought by enhancing nutrient uptake and increasing the synthesis of important secondary metabolites such as caryophyllene and linalool.	(Fatemi et al. 2025)
<i>Bacillus</i> spp.,	<i>Lactuca sativa L</i>	Drought	- Highest growth when compared to plants that were not inoculated during drought conditions. - Treatments led to higher biomass production and were closely linked to improved photosynthetic activity, water status, chlorophyll content, and N-uptake.	(Santander et al. 2024)
<i>Pseudomonas</i> sp. and <i>Pantoea</i> sp.	<i>Hordeum vulgare</i>	Drought	- The soil carbon flux, net photosynthetic rate, chlorophyll levels, and stomatal conductance of inoculated plants were all noticeably greater. - Lowers the possibility of oxidative stress, minimizes damage to membranes, and shields plants from oxidative defenses.	(Abideen et al. 2022)

concentrations, which alter plants' physiology, biochemistry, and molecular makeup to help them withstand drought (Spence et al. 2014).

Under stressful conditions, bacterial inoculation decreased ROS and lipid peroxidation levels while increasing plant biomass and chlorophyll content

(Vaishnav et al. 2019) (Fig. 3). Comparing bacterially inoculated plants to non-inoculated plants, the former showed increased levels of antioxidant enzymes (GR, POD, CAT, and SOD), non-enzymatic antioxidants (glutathione and ascorbic acid), and total phenol content (Vaishnav et al. 2019). In this context, to test

cross-species bacterial-mediated stress alleviation, Pandey et al. (2012) inoculated cucumbers with the wheat endophytic bacterium *Pseudomonas aeruginosa* PW09; application of this strain improved the activity of defense enzymes, namely polyphenol oxidase and SOD, under salt stress and resulted in an augmentation of total phenolic content and free proline.

Endophytic bacteria are essential for plants to withstand salt and water stress (Table 4).

Conclusion

Abiotic stresses, such as water stress and salinity, can impede the growth and development of aromatic and medicinal plants, which alters their physiological and biochemical homeostasis. One of the many approaches proposed to deal with stress includes plant-microbe interactions. By using this approach, plants can produce secondary metabolites and increase levels of non-enzymatic and enzymatic antioxidants that help protect and defend them against continuous stress attacks. The ability of bacterial and fungal endophytes to confer stress tolerance on plants could provide a new strategy for mitigating the adverse effects of various abiotic stresses on agricultural production.

Abbreviations

ROS	Reactive Oxygen Species
CAT	Catalase
APX	Ascorbate Peroxidase
GR	Glutathione Reductase
SOD	Superoxide Dismutase
MDA	Malondialdehyde
RWC	Relative Water Content
ABA	Absciscic Acid
PGPB	Plant Growth-Promoting Bacteria
SA	Salicylic Acid
IAA	Indole-3-Acetic Acid
POD	Peroxidase
H ₂ O ₂	Hydrogen Peroxide
GPX	Guaiacol Peroxidase
MDHAR	Monodehydroascorbate Reductase
PAL	Phenylalanine Ammonia-Lyase
PPO	Polyphenol Oxidase
GR	Glutathione Reductase
AAO	Ascorbate Oxidase

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Authors' contributions

Hamza EL KISSANY conducted the literature search, analysis, and drafting of the manuscript. Hicham EL-BOUKHARY and Adil LAAZIZ contributed to the critical review and structuring of the content. Abdelouahed HAJJAJI

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Data availability

Since this study is a literature review, all data supporting the findings are contained within the article itself. No additional raw data were generated. Further information is available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

This article is a literature review and does not contain any studies with human participants or animals performed by any of the authors. Therefore, ethical approval is not required.

Consent for publication

Not applicable. This manuscript is a literature review and does not include any individual person's data in any form that would require consent for publication.

Competing interests

The authors declare that they have no relevant financial or non-financial interests to disclose related to the content of this article.

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