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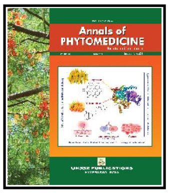

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Endophytic associations in Zingiberaceae: Impact on plant health

A. Kamini, S. Sundravadana*◆, E. Rajeswari, M. Gnanachitra*** and K. Chandrakumar******

**Department of Spices and Plantation Crops, Tamil Nadu Agricultural University, Coimbatore-641003, Tamil Nadu, India*
*** Department of Plant Pathology, Tamil Nadu Agricultural University, Coimbatore-641003, Tamil Nadu, India*
**** Department of Agricultural Microbiology, Tamil Nadu Agricultural University, Coimbatore-641003, Tamil Nadu, India*
***** Department of Plant Molecular Biology and Bioinformatics, CPMB and B, Tamil Nadu Agricultural University, Coimbatore-641003, Tamil Nadu, India*

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Abstract

Zingiberaceae includes some notable economically and medicinally significant plants such as turmeric (*Curcuma longa* L.), ginger (*Zingiber officinale* Rosc.) and cardamom (*Elettaria cardamomum* L.), which are distinguished by their aromatic rhizomes, sheathed leaves and intricate inflorescences with vibrant bracts. They are highly valued for their medicinal, culinary, aromatic and ornamental properties. The successful cultivation of Zingiberaceous crops is found to be difficult due to fungal and bacterial infections. Managing diseases by chemical methods has proven to be effective, but it may cause environmental hazards. The high diversity of endophytes in Zingiberaceae presents opportunities for their use in ecologically friendly and sustainable agricultural practices. It represents a prolific, abundant source of bioactive chemical compounds with major uses in the pharmaceutical and agrochemical industries. These compounds exhibit diverse biological activities, including antimicrobial, antifungal, antioxidant, antiparasitic, immunosuppressive and insecticidal properties. Furthermore, endophytes play crucial roles in producing siderophores, synthesizing indole-3-acetic acid, solublizing phosphorus and assimilating nitrogen and contributing significantly to plant growth and soil health. This review explains many important roles of endophytes in plants from the Zingiberaceae family. It focuses on how these helpful microbes support plant growth, protect plants from diseases and produce natural compounds that can be used in medicine and agriculture. It covers aspects such as their roles in plant growth promotion, disease suppression, volatile compounds production, and exhibition of various biological activities.

1. Introduction

Endophytic microbes are naturally occurring microorganisms that inhabit plant tissues and play a crucial role in protecting against various plant pathogens and contributing to plant health. Their importance extends beyond pathogen defense, as they enhance agricultural productivity and ecological balance by promoting plant growth, improving stress tolerance and aiding in nutrient acquisition. This symbiotic relationship highlights the broader significance of endophytic microbes in sustainable agriculture and environmental conservation. These microbes reside within plant tissues and substantially promote plant growth and development by supporting homeostasis and protecting against adverse environmental conditions, such as heavy metal stress and drought tolerance (Khan *et al*., 2019). Furthermore, they facilitate improved nutrient uptake, suppress weed growth and activate both induced systemic resistance (ISR) and systemic acquired resistance (SAR), thereby strengthening plant defense against pathogens and pests (Irizarry and White, 2018). In the Zingiberaceae family, endophytic microbes are crucial for enhancing plant growth, development and biosynthesis of bioactive secondary compounds (Chakraborty *et al*., 2019). Endophytic microbes colonize plants primarily through horizontal transfer from the soil. In their initial stages, these microbes derive nutrition and shelter from the host while enhancing the host's tolerance to viruses, herbivores and other abiotic stresses (Verma *et al*., 2017). Based on their colonization activity, endophytic microorganisms are categorized as either facultative or obligate. Facultative endophytes can colonize plants at various life cycle stages and interact with the host's rhizosphere soil. Organic compounds released from the plant's rhizosphere zones and root secreted substances, including carbohydrates, amino acids and various secondary metabolites, act as chemoattractant, enabling signal transmission and microbial attraction (Rozpadek *et al*., 2018). The environment and geographic location of the host plant also significantly influence the composition and population of endophytic microbes (Ferdous *et al*., 2019).

Zingiberaceae family, commonly called as the ginger family, is renowned for its economic and ecological significance, playing a vital role in traditional medicine, culinary practices and ornamental horticulture. This diverse group of flowering plants includes approximately 1,300 species classified into 52 genera, making it one of the largest and most varied plant families (Kaliyadasa and Samarasinghe, 2019). These plants are widely distributed across tropical regions, particularly in Southeast Asia (Saboo *et al*., 2014). Species like *Zingiber* serve as essential ingredients in traditional

Corresponding author: Dr. S. Sundravadana
Associate Professor, Department of Spices and Plantation Crops, Tamil Nadu Agricultural University, Coimbatore- 641003, Tamil Nadu, India
E-mail: sundravadana.s@tnau.ac.in
Tel.: +91-9488976761

Email: ukaaz@yahoo.com; Website: www.ukaazpublications.com

medicinal tonics such as "Jamu," which are widely produced and commercially sold in Malaysia and Indonesia (Habsah *et al*., 2000). The Zingiberaceae family serves both culinary and ornamental purposes, with major genera including *Zingiber* (49 species), *Kaempferia* (17 species), *Hedychium* (22 species), *Curcuma* (34 species), *Globba* (42 species), *Alpinia* (17 species), *Amomum* (16 species), *Etlingera* (12 species) and *Caulokaempferia* (14 species) (Rachkeeree *et al*., 2018). Among these genera, turmeric (*Curcuma longa* L.), ginger (*Zingiber officinale* Rosc.) and cardamom (*Elettaria cardamomum* L.) are economically significant due to their extensive cultivation and commercial value. Many Zingiberaceae species, known for their fragrant, long-lived herbs with creeping or tuberous rhizomes, are of considerable economic importance for their applications in producing spices, ornamental plants and traditional medicines. Additionally, these plants are rich sources of export-quality oleoresins and volatile essential oils (Chakraborty *et al*., 2019). In the last 16 years, endophytes associated with the Zingiberaceae family have been identified as sources of a wide variety of metabolites exhibiting notable biological properties. These include antimicrobial and antioxidant compounds like volatile organic compounds and phenolic acids; anti-inflammatory agents such as polyketides and flavonoids and alkaloids and hybrid terpenes. Alkaloids are known for their anticancer properties. Additionally, peptides and aromatic compounds from these endophytes contribute to the pharmaceutical and cosmetic industries (Ariantari *et al*., 2019). Genera like *Curcuma*, *Kaempferia*, *Hedychium*, *Amomum*, *Zingiber* and *Elettaria* exhibit significant bioactivities including antimicrobial, anti-inflammatory, antioxidant and anticancer effects (Taechowisan *et al*., 2008). Furthermore, Zingiberaceae plants contain abundant phytochemicals like diarylheptanoids, flavonoids, phenolic acids and alkaloids, which have vast potential in pharmaceutical, essential oil, dye, perfume and cosmetic industries. The rising cultivation area and production volume between 2018 and 2023 underscore the growing economic importance of this plant family. For optimal yield, planting healthy, pathogen-free and ideally pre sprouted rhizomes is essential for early and robust growth (Fisher *et al*., 2023)

2. Intrusion of endophytes

Endophytes are key contributors to enhancing plant growth, health and resistance by colonizing plant tissues intercellularly or intracellularly. Bacterial endophytes primarily gain entry through natural plant openings, such as lateral root emergence sites or root elongation zones (Hardoim *et al*., 2008). In contrast, fungal endophytes employ both vertical and horizontal transmission strategies: vertical transmission occurs through the transfer of endophytes from maternal plants to progeny seeds, whereas horizontal transmission often involves the introduction of fungal spores facilitated by herbivory or insect vectors (Rodriguez *et al*., 2009). These microorganisms can act as commensals (neutral partners), pathogens (disease-causing agents), saprotrophs (decomposers) or mutualistic symbionts. In addition, AGPs (arabinogalactan proteins), classified under the hydroxyproline-rich glycoprotein (HRGP) superfamily, play a crucial role in plant-microbe interactions at various colonization stages by acting as microbial attractants or repellents and contributing to the formation of pathogenic structures (Nguema Ona *et al*., 2013). Apart from AGPs, other root secretions such as organic acids, amino acids, phenolic compounds, sugars and various bioactive compounds selectively attract mutualistic microbes, including endophytes (de Oliveira Chagas *et al*., 2017). The diversity of endophytes associated with Zingiberaceae is presented in Table 1. Recent research highlights the importance of these interactions for plant survival and maintaining ecological balance. When an endophyte enters a plant, it recognizes the host and communicates via distinct chemical signals (Ali *et al*., 2014). Scientific studies indicate that endophytes are responsive to root exudates, nutrient and water-rich substances secreted by plant roots, which facilitate microbial recruitment. Specific compounds within these exudates, such as flavonoids, enhance the attraction of compatible microbes and enable endophyte-plant root interactions (Das and Varma, 2009). Endophytes can regulate host plant defense-related signalling pathways, enabling colonization and symbiotic relationship establishment. This process involves microbial-associated molecular patterns (MAMPs), which encompass molecules like β-chitosan, bacterial cold shock protein (RNP1 motif), PG, SOD, EF-Tu and chitin, along with the host-specific recognition by cell surface pattern recognition receptors (PRR) molecules (Newman *et al*., 2013). Research has demonstrated two primary effects of endophytes on plants. Endophytes can induce systemic resistance (ISR) in hosts, which differs from the more widely studied systemic acquired resistance (SAR). While ISR and SAR exhibit similar phenotypes, induced systemic resistance (ISR) offers wide-ranging protection against plant pathogens (Sharma *et al*., 2024). ISR is primarily characterized by its reliance on the jasmonic acid (JA) signalling pathway during symbiotic interactions, facilitating quicker, more robust and sustained defense responses under stressful conditions (Teixeira *et al*., 2019). The precise mechanism behind the 'priming' state remains unclear, transcription factors and associated signalling molecules are thought to play pivotal roles. Ongoing molecular interactions between endophytes and their hosts, especially those mediated by JA pathway, significantly influence the activation of plant immunity and associated defense mechanisms (Bastias *et al*., 2017). Endophyte infection can suppress the salicylic acid (SA) pathway, increase JA precursor levels and upregulate JA response genes (Zhang *et al*., 2008). Previous studies suggest that increased activity in JA pathway is closely linked to the establishment and function of mycorrhizal symbiosis. However, further research is necessary to fully elucidate this relationship. The nature of interaction and colonisation between host plants and endophytes is greatly shaped by the involvement of specific types of endophytes (Clay and Schardl, 2002). Additionally, some endophytic fungi secrete cell wall-hydrolysing enzymes, including cellulases, hemicellulases and pectinases, which break down specific components of the plant cell wall, facilitating their penetration of plant tissues and overcoming initial plant defense barriers (Schulz and Boyle, 2005). Plants have chitin-specific receptors known as PR-3, identifying chitin oligomers found in fungal cell walls, activating the plant's immunological responses to possible fungal invasion (Sánchez-Vallet *et al*., 2015). However, certain fungal endophytes have evolved complex mechanisms to evade detection. Notably, they generate the enzyme chitin deacetylase, which transforms chitin oligomers into chitosan, a modified form that the plant's receptors cannot detect. This metabolic change allows the fungi to avoid activating the plant's defense mechanism, allowing them to form symbiotic or endophytic relationships without attack (Cord-Landwehr *et al*., 2016). Intrusion of plant-beneficial endophytes in the Zingiberaceae is shown in Figure 1.

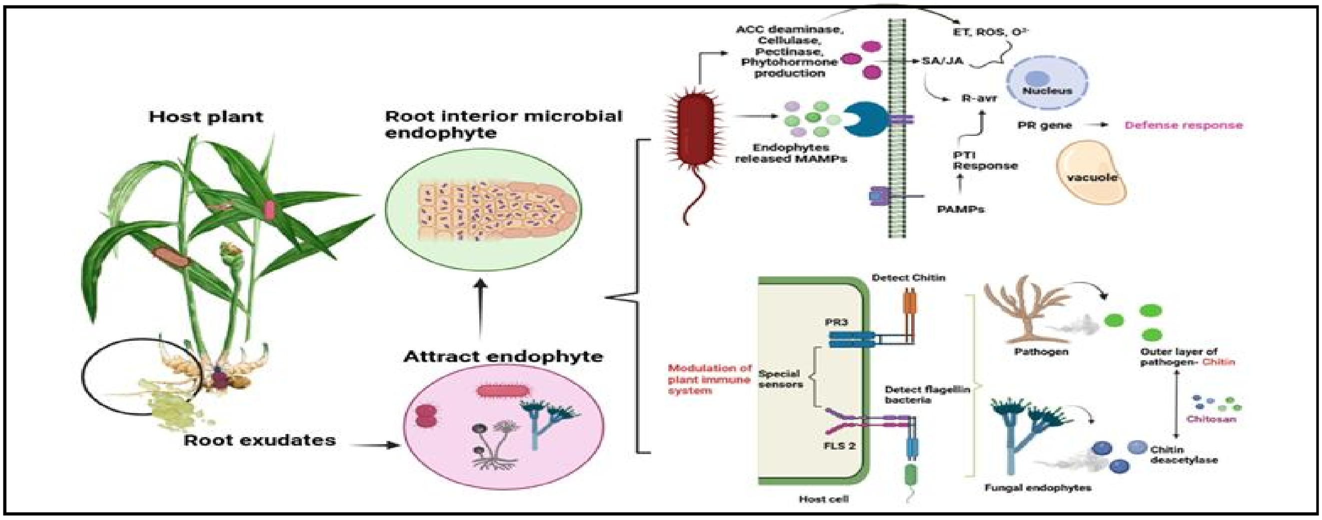

Figure 1: Illustration of plant-beneficial endophytes intrusion in the Zingiberaceae family (Created by using biorender).

Table 1: Exploration of endophytes diversity in Zingiberaceae-associated plants

Crop	Endophytic microorganisms		References
	Fungi	Bacteria	
Turmeric (*Curcuma longa*)	*Arthrobotrys foliicola*, *Fusarium verticillioides*, *Fusarium solani*, *Fusarium oxysporum*, *Fusarium proliferatum*, *Phaeosphaeria ammophilae*, *Cochliobolus kusanoi*	*Bacillus thuringiensis*, *Bacillus pumilus*, *Bacillus cereus*, *Bacillus safensis*, *Clavibacter michiganensis*, *Pseudomonas putida*	Deshmukh *et al.*, 2018
Pale turmeric (*Curcuma heyneana*)	-	*Bacillus aerophilus*, *Sphingomonas* sp., *Agrobacterium tumefaciens*, *Herbaspirillum* sp., *Agrobacterium larrymoorei*, *Microbacterium testaceum*, *Enterobacter cancerogenus*, *Chromobacterium aquaticum*, *Rhizobium alamii*, *Enterobacter asburiae*	Sulistiyani and Lisdiyanti, 2016
Javanese turmeric (*Curcuma xanthorrhiza)*	*Eupenicillium* sp., *Fusarium oxysporum*, *Fusarium solani*, *Xylaria* sp.	-	Hammerschmidt *et al.*, 2015
Ginger (*Zingiber officinale*)	*Aspergillus niger*, *Fusarium* sp., *Cochliobolus geniculatus*, *Colletotrichum gloeosporioides*, *Talaromyces assiutensis*, *Rhizopycnis vagum*, *Gliocladiopsis*, *Trichothecium* sp., *Colletotrichum crassipes*, *Fusarium solani*, *Fusarium oxysporum*, *Acremonium furcatum*, *Acremoniumm acroclavatum*, *Glomerella cingulata*	*Streptomyces aureofaciens*	Ginting *et al.*, 2013
Blue ginger (*Alpinia galanga*)	-	*Micromonospora, Microbispora, Streptomyces* sp. LJK109, *Streptomyces* sp. Tc022	Thongchai *et al.*, 2012
Malacca ginger (*Alpinia malaccensis*)	*Cladosporium oxysporum*, *Penicillium citrinum*, *Diaporthe gardenia*, *Colletotrichum boninense*, *Colletotrichum gloeosporioides*, *Pyricularia costina*, *Colletotrichum cliviae*, *Aspergillus flavipes*	-	Uzma *et al.*, 2016
Lesser galangal (*Alpinia officinarum*)	*Exserohilum* sp., *Fusarium oxysporum*, *Penicillium herquei*, *Pestalotiopsis* sp., *Colletotrichum siamense*	-	Hartanto *et al.*, 2019
Finger root (*Boesenbergia rotunda*)		*Asanoa endophytica*, *Streptomyces* sp.	Taechowisan *et al.*, - 2017
Cardamom (*Elettaria cardamomum* Maton)	*Piriformospora indica*	-	Anjana *et al.*, 2023

3. Endophytes as plant growth promoters in the Zingiberaceae family

Endophytic microbes support plant growth by regulating hormones and enhancing nutrient uptake, promoting development under both optimal and stressful conditions (Ma *et al*., 2016). These microbes directly enhance plant growth and yield by producing phytohormones (IAA, gibberellins, cytokinins), solubilising phosphate, fixing nitrogen, suppressing pathogens (Reshma *et al*., 2018), improving stress tolerance (Sagar *et al*., 2020) and boosting nutrient availability (Liu *et al*., 2016). Malisorn *et al*. (2021) isolated endophytic bacteria from Zingiberaceae, including *Bacillus*, *Lysinibacillus*, *Kerstersia*, *Klebsiella* and *Brucella* are identified through 16S rRNA sequencing and phenotypic traits. They reported the ability of all the isolates to produce IAA, nitrogen fixation and zinc/phosphate solubilization abilities by some of the isolates. Moreover, Zhang *et al*. (2018) isolated 57 bacterial strains, classified into genera such as *Tetrobacter*, *Enterobacter*, *Acinetobacter*, *Pseudomonas*, *Stenotrophomonas*, *Agrobacterium* and *Bacillus* via 16S rDNA PCR-RFLP. Out of 34 tested strains, several showed PGP traits: 14 produced IAA, 18 showed siderophore activity and 19 solubilised phosphates. Six strains exhibited strong plant growth-promoting potential. Likewise, Bódalo *et al*. (2023) identified 19 endophytes of bacterial strains recovered from ginger rhizomes (*Zingiber officinale* Rosc.), including *Lysinibacillus*, *Agrococcus*, *Acinetobacter*, *Kocuria*, *Agrobacterium*, *Zymobacter*, *Lelliottia* and *Mycolicibacterium*. As well, *L. amnigena* J29 showed multiple PGP traits, while strains like *Mycolicibacterium* sp. J5, *A. citreus* J28 and *L. capsici* J26 demonstrated nitrogen fixation and siderophore production. Growth-promoting activity of endophytes in Zingiberaceae is furnished in Table 2.

Table 2: Endophytes-mediated plant growth promotion in Zingiberaceae family

Host	Phytohormone generation	Fungal endophytes	Bacterial endophytes	References
Ginger (*Zingiber officinale*)	ACC deaminase, ethylene-inducing stresses	-	*Pseudomonas* sp. strains	Jasim *et al*., 2014
Z. officinale	IAA, siderophore and phosphate solubilising activity	-	Bacteria (GS2, GS5, GS8 and GS10)	Jabborova *et al*., 2020
Z. officinale (Leaves)	Harzianic acid and isoharzianic acid compounds	*Trichoderma harzianum*	-	Harwoko *et al*., 2021
Z. officinale	IAA, gibberellin and cytokinin	-	*Bacillus endophyticus, funneliformis mosseae*	Jabborova *et al*., 2022
Curcuma longa (Rhizome)	Curcumin, IAA enhanced the root and shoot length	-	*Azotobacter chroococcum*	Virk *et al*., 2023
C. longa	IAA, gibberellic acid	-	*Bacillus* and *Pseudomonas*	Jadhav, 2024
C. xanthorrhiza	IAA, ammonia, ACC deaminase, catalase, hydrolytic enzymes, exopolysaccharide and nitrogen fixation	-	*B. cereus* and *P. aeruginosa*	Saryanah *et al*., 2021
Elettaria cardamomum Small cardamom	Auxin and IAA	*Piriformospora indica* and *Glomus fasciculatum*	-	Aishwarya *et al*., 2022
E. cardamomum	Phosphate solubilization, nitrogen fixation, ACC deaminase and enzyme activity	-	EcB 2 (*Pantoea* sp.), EcB 7 (*Polaromonas* sp.), EcB 9 (*Pseudomonas* sp.), EcB 10 (*Pseudomonas* sp.)	Jasim *et al*., 2015
Java cardamom (*Amomum compactum*) and bitter ginger (*Zingiber zerumbet*)	Phosphate solubility, nitrogen fixation and cellulolytic action	-	*Priestia megaterium*, *Pr. aryabhattai* and *Paenibacillus tyrfis*	Geraldi *et al*., 2024

4. Diseases suppression by endophytes in Zingiberaceae

Endophytes, including bacteria and fungi, are beneficial microorganisms that reside within plant tissues without causing disease, playing a vital role in plant defense. They suppress pathogens through direct mechanisms like antimicrobial compound production (*e.g.*, antibiotics, enzymes and secondary metabolites) and indirect strategies that enhance plant immunity (White *et al*., 2019). Moreover, 30 endophytic fungal strains were obtained from red ginger and identified as *Acremonium macroclavatum*, *Fusarium solani*, *Curvularia affinis* and *Glomerella cingulata*. Antifungal assays against *Fusarium oxysporum* showed varied inhibition (1.4-68.8%) with *F. solani*, *G. cingulata* and *C. affinis* displaying the highest activity (Ginting *et al*., 2013). Additionally, 31 endophytes isolated from turmeric were identified using morphological characteristics and ITS-rDNA sequencing. Their antifungal activity was tested against *Pythium aphanidermatum* and *Rhizoctonia solani*, the pathogens responsible for causing rhizome rot and leaf blight, respectively. Among them, six isolates showed strong antagonistic activity, inhibiting pathogen growth by over 70%. In particular, *Trichoderma harzianum* Thar DOB-31 effectively suppressed *P. aphanidermatum* (76.0%) and *R. solani* (76.9%) *in vitro* using dual inoculation experiments (Vinayarani and Prakash, 2018). Keerthi *et al.* (2016) isolated a total of 34 endophytes from *Z. zerumbet* rhizomes and identified them as *Fusarium solani* (7 isolates), *F. oxysporum* (2 isolates) and *Rhizobium* sp. (1 isolate) by molecular analysis (ITS/16S rRNA). The study also confirmed the antagonistic potential of endophytic fungi against *Pythium myriotylum*. According to their morphological traits, 32 endophytic fungi were identified from the rhizomes of six Zingiberaceae species in Karanganyar, Central Java, Indonesia. Non-eluted TLC bioautography revealed that several endophytic fungal extracts exhibited antibacterial activity against *Staphylococcus aureus* Ina-CC B4 and *Escherichia coli* Ina-CC B5, along with notable DPPH antioxidant activity (Praptiwi *et al*., 2016). Similarly, 11 bacterial isolates were recovered from the roots of torch ginger (*Etlingera elatior*), comprising seven Gram-negative and four Gram-positive strains. Antifungal assays showed that some isolates inhibited fungal growth, with IAK3, IAK9 and IAK11 selected for further testing due to their strong activity. Notably, the ethyl acetate extract of IAK9 effectively inhibited *Rhizoctonia solani*, while the n-hexane extract of IAK11 showed strong inhibition against *R. microporus* (Suryanto *et al*., 2016). Six endophytic bacterial strains obtained from different ginger species, collected from diverse states in India's North Eastern Hill (NEH) region, were evaluated for their antagonistic activity against *Pythium* sp., the causal agent of ginger soft rot. Dual culture assays showed that all isolates inhibited the mycelial growth of the pathogen *Alcaligenes* sp. (GE-1) exhibited the highest inhibition (80.98%), followed by *Bacillus* sp. GE-4 (78.89%) and GE-5 (77.33%). Among the isolates, *Bacillus* sp. GE-3 (64.89%) showed the lowest level of inhibition. Four isolates demonstrated more than 70% inhibition, indicating their strong potential for use in consortia to manage ginger soft rot under field conditions (Bamon *et al*., 2018). From the samples, 44 endophytes were successfully recovered from *Zingiber cassumunar*, among which *Arthrinium* sp. MFLUCC16-1053 showed notable antibacterial properties. The ethyl acetate extract of this isolate showed inhibitory effects on both Gram-positive and Gram-negative bacteria. In addition, multiple bioactive compounds with antibacterial and antioxidant activities were identified through chemical analysis, including γ-curcumene, β-cyclocitral, β-isocomene, 3E-cembrene A, laurenan-2-one, sclareol, 2Z, 6E-farnesol and cembrene (Pansanit and Pripdeevech, 2018). Moreover, Soe and Wint (2020) isolated fungal endophytes from various Zingiberaceae plants, including *Aspergillus* sp. from *Hedychium flavum*, *Penicillium* sp. from *Zingiber officinale* Rosc., *Mucor* sp. from *C. longa* and *Trichoderma* sp. from *Alpinia galanga*. Among them, *Trichoderma* sp. (S6) showed the strongest antimicrobial activity, producing 25 mm inhibition zone against *Bacillus subtilis*, 23 mm against *E. coli* and slight inhibition (10-11 mm) of *Candida albicans*. Similarly, six endophytic bacterial strains were isolated from *Curcuma aeruginosa*, *C. xanthorrhiza* and *C. zedoaria*, all demonstrating potential antibacterial activity. Among them, *Bacillus amyloliquefaciens* from *C. xanthorrhiza* (Temulawak) exhibited the strongest inhibition against both Methicillin-resistant *Staphylococcus aureus* (MRSA) and *Klebsiella pneumoniae*. Additionally, two *Bacillus* strains from *C. aeruginosa* (Temu Putih) showed moderate activity against *K. pneumoniae*, though with smaller inhibition zones. These findings highlight the potential of Curcuma-derived endophytes as sources of antibacterial agents (Indrawati *et al*., 2018). Plant diseases inhibited by the endophytes in Zingiberaceae are presented in Table 3.

Table 3: Plant disease suppression by endophytes in the Zingiberaceae family

Host plant	Fungal endophytes	Bacterial endophytes	Pathogens suppressed by endophytes in Zingiberaceae	References
Zingiber zerumbet	-	*Klebsiella aerogenes*	*Pythium myriotylum*	Harsha and Nair, 2020
Z. officinale	*Aspergillus terreus*	-	*Colletotrichum gloeosporioides*	Gupta *et al*., 2022
Z. officinale	-	*Enterobacter arburiae* and *Pseudomonas indica*	*Ralstonia solanacearum*	Dang *et al*., 2023
Z. zerumbet	-	ZzER11 (*B. amyloliquefaciens*) and ZzER62 (*B. subtilis*)	*Pythium myriotylum*	Princy *et al*., 2023
Z. officinale	-	*Bacillus licheniformis*	*P. myriotylum*	Alarjani and Elshikh, 2024
Torch ginger (*Etlingera* sp.), Wild forest ginger (*Globba patens*), *Globba pendula* and *Zingiber multibracteata*	-	Proteobacteria EZS06	EPEC (*Escherichia coli*), *P. vulgaris* ATCC 13315 and *L. monocytogenes* BTCC B693.	Mamangkey *et al*., 2020
	-	EZS20	*Staphylococcus aureus* ATCC 29213, EZS28	
	-	EZS28	*S. aureus* (MRSA)ATCC 43300	
	-	EZS45	*S. epidermidis* ATCC 12228	

Torch ginger (*Etlingera elatior*)	*Trichoderma* sp. and *Pestalotiopsis* sp.	-	*F. oxysporum, Ganoderma boninense,* and *Rigidoporus lignosus*	Lutfia *et al.,* 2020
Zingiber officinale Rosc.	-	*Lysinibacillus, Agrococcus, Acinetobacter, Agrobacterium, Lelliottia, Kocuria* and *Mycolicibacterium*	*Botrytis cinerea* and *Colletotrichum acutatum*	Bódalo *et al.,* 2023
Turmeric (*Curcuma longa*)	-	*B. subtilis* IJ10 and *Pseudomonas* sp. IJ2	*F. solani* FS-01 and *Pythium aphanidermatum* (ITCC 7908)	Kharshandi and Kayang, 2023

5. Volatile compounds of endophytes from Zingiberaceae

An investigation of endophytic microbes isolated from the Zingiberaceae family revealed the presence of several bioactive volatile organic compounds (VOCs), such as tyrosol, benzeneacetic acid, dehydromevalonic lactone and a range of fatty acids, including n-hexadecanoic acid and linoleic acid (Anisha and Radhakrishnan, 2017). The production of these VOCs by endophytic microbes highlights their potential in enhancing plant defense mechanisms and their applicability in sustainable agricultural practices (Kaddes *et al.*, 2019). Furthermore, Taechowisan *et al.* (2014) reported that *Streptomyces* sp. strain BT01, isolated from the root tissue of *Boesenbergia rotunda*, is a producer of several volatile organic compounds (VOCs) and has potent antibacterial activity against Gram-positive bacteria, such as *Staphylococcus aureus*, *Bacillus cereus* and *Bacillus subtilis*. Through bioassay-guided fractionation, two novel flavonoids- 7-methoxy-3,3 2 ,42 ,6-tetrahydroxyflavone and 22 ,7-dihydroxy-42 ,52 -dimethoxyisoflavone were identified along with four known compounds, all exhibiting MIC values ranging from 32 to 256 µg/mL. In another way, the endophytic fungus *Arthrinium* sp. MFLUCC16-1053, isolated from *Zingiber cassumunar*, exhibited strong antibacterial activity against *Staphylococcus aureus* and *Escherichia coli*, with minimum inhibitory concentrations of 31.25 and 7.81 µg/mL, respectively. Additionally, GC-MS analysis revealed that its major volatile compounds included β-cyclocitral, β-isocomene, γ-curcumene, 2Z,6E-farnesol, cembrene, sclareol, laurenan-2-one and 3E-cembrene A (Pansanit and Pripdeevech, 2018). Endophytic bacteria, including *Enterobacter*, *Pantoea* and *Klebsiella*, were isolated from the rhizomes of *Zingiber zerumbet*. Among them, *Klebsiella aerogenes* isolate ZzKSD8 exhibited the strongest antagonistic activity against *Pythium myriotylum*. Methanol extracts revealed key compounds such as cyclopropane octanoic acid, methyl palmitate (31.37%), 2-hexyl-methyl ester (17.05%) and methyl stearate (18.57%). Ethyl acetate extracts contained alkanes like 2-methyloctacosane (12.10%) and tetra tetracontane (13.18%), while ethanolic extracts were rich in 4,22-sigmastadiene-3-one (22.51%) and stigmast-5-en-3-ol (3β) (17.40%) (Harsha and Nair, 2020). A more recent study by Das *et al.* (2020) identified eleven fungal endophytes from *Zingiber nimmonii* by ITS sequencing and screened for antibacterial activity. Ethyl acetate extracts from nine isolates showed activity, with *Bipolaris specifera* showing the highest inhibition (MIC: 0.04- 0.14 mg/ml). Seven antibacterial compounds, mainly volatile esters and phenolics, were identified. These results suggest potential for novel drug discovery from endophytes of medicinal plants. Additionally, volatile compounds from Zingiberaceae species have demonstrated notable antibacterial and antioxidant activities. In a study, 48 bacterial endophytes were isolated from the turmeric rhizosphere and screened *in vitro* for their antagonistic activity, inhibiting *Fusarium solani* FS-01 and *Pythium aphanidermatum* (ITCC 7908), along with analysis of their VOC production and enzymatic activity (Kharshandi and Kayang, 2023). Volatile compounds produced by endophytes associated with Zingiberaceae is shown in Table 4 and Figure 2.

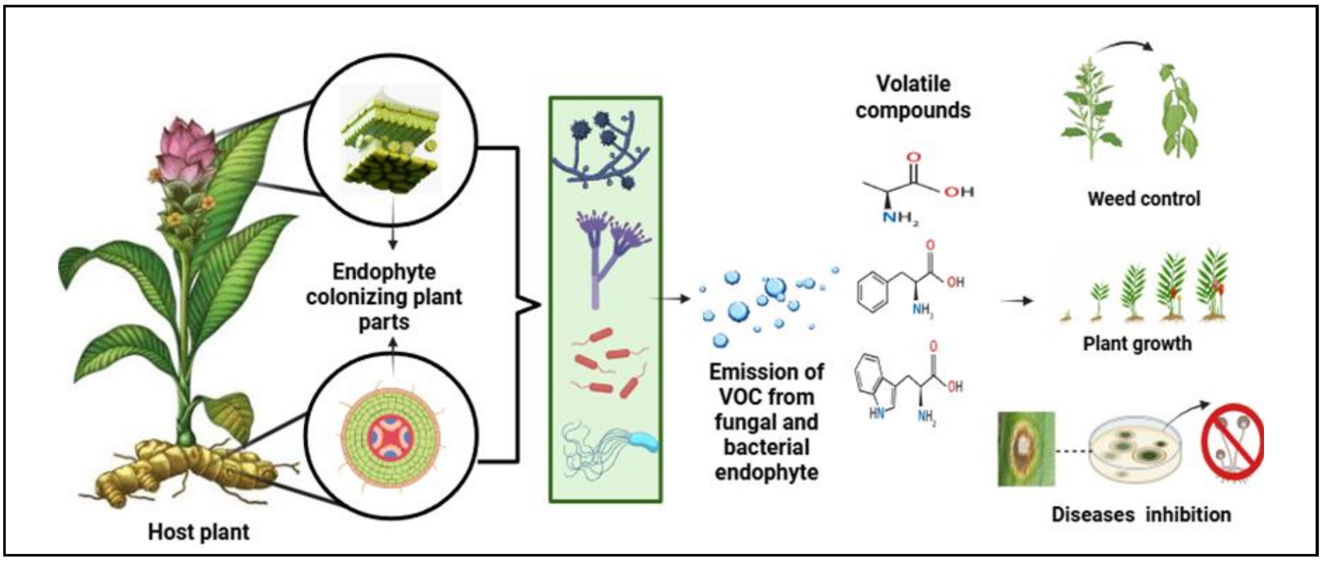

Figure 2: Diagrammatic representation of volatile compounds produced by endophytes in Zingiberaceae (Created by using biorender).

Table 4: Volatile compounds produced by endophytes of the Zingiberaceae family

Volatile compounds	Fungal endophytes	Bacterial endophytes	Host species	References
Lactate dehydrogenase, malondialdehyde	-	*Bacillus cereus*- strain SZ-1	*Artemisia annua*	Zheng *et al*., 2016
Ergosta-4, 6, 8(14), 22-tetraen-3-one (ergone)	GF6 (*Gliocladiopsis*)	-	*Z. officinale*	Anisha and Radhakrishnan, 2017
α-muurolol, β-bisabolenol, 3E-cembrene A, γ-curcumene, 3-pmenthone and 11,12-dihydroxy-valencene	*Arthrinium* sp. MFLUCC16-1053	-	*Z. cassumunar*	Pansanit and Pripdeevech, 2018
Punctaporin B Sapindoside A	*Arthrinium* sp. MFLUCC16-1053	-	*Curcuma longa*	Pansanit and Pripdeevech, 2018
2-Methyl-2E-hexenoic acid, 2-oxo-3-methylvaleric acid	*T. harzianum* TharDOB-31	-	*C. longa*	Vinayarani and Prakash, 2018
Trans-cinnamic acid, 1-heptacosanol	-	*Nocardiopsis* sp.	*Z. officinale*	Sabu *et al*., 2018
Aminopyrrolnitrin oxidase gene	-	*Serratia* sp. ZoB14	*Z. officinale*	Sabu *et al*., 2019
1-hydroxy-2-methyl-6-methoxyanthraquinone and 6-methoxy-2-methylquinizarin	-	*Bacillus cereus, B. subtilis, Staphylococcus aureus* and methicillin-resistant *S. aureus*	*Amomum* sp.	Taechowisan *et al*., 2021
Griffithiene, scalaradial, methicillin	*Hyomontagnella monticulosa* strain Zg 15SU	-	*Z. griffithii*	Lutfia *et al*., 2021

6. Biological activity of endophytes associated with Zingiberaceae

6.1 Anticancer and anti-inflammatory activity

Endophytes isolated from Zingiberaceae species, in particular, have shown excellent anticancer and anti-inflammatory properties, making them potential candidates to support the discovery of novel natural treatments (Kharwar *et al*., 2011). A total of 563 endophytic fungi were isolated from *Z. officinale*, with the most bioactive fungi namely *Aspergillus terreus.* It produced terrein, a chemical with potent antibacterial, antifungal and cytotoxic effects. Furthermore, terrein extracted from *A. terreus* was found to possess antibacterial as well as anticancer effects (Ariantari *et al*., 2024). In a similar study, Ningrum *et al.* (2017) reported that isolation of endophytic fungi from turmeric (*Curcuma longa* L.) collected in Sukabumi and Cibinong and examined for antioxidant and anticancer properties. Four endophytic fungi from turmeric with major antioxidant activity (>70%) inhibited the growth of MCF-7 breast cancer cells proportionally to the dose, with IC_{50} values from 446 to 579 ppm. These isolates have potential anticancer activities. Additionally, *Streptomyces zerumbet* W14, a new endophytic species of *Zingiber zerumbet*, was identified using morphology and 16S rDNA analysis. They identified two bioactive compounds, such as methyl 5-(hydroxymethyl) furan-2-carboxylate and geldanamycin. Compound 1 demonstrated high antibacterial activity (MIC as low as 1 µg/ml), while compound 2 reduced pro-inflammatory indicators. These findings indicated that there is potential for treating bacterial infections and inflammation (Taechowisan *et al*., 2019). In the same vein, Jalgaonwala and Mahajan, (2014) isolated *Eurotium* sp., an endophytic fungus from *C. longa* rhizomes and evaluated it for asparaginase production. Maximum enzymatic activity was observed at 40°C and a pH of 8.0, with a molecular weight of 14.3 kDa. Asparaginase was reported for the first time as a source of the anticancer enzyme.

6.2 Antioxidant activity

Antioxidant activity is the process by which bioactive compounds neutralize free radicals, particularly reactive oxygen species (ROS), thereby mitigating oxidative damage at the cellular level. In Zingiberaceae plants, this activity plays a crucial role in enhancing resilience against environmental stressors, safeguarding against pathogen attacks and slowing down aging processes by maintaining oxidative balance (Dumanoviæ *et al*., 2021). Correspondingly, Praptiwi *et al.* (2016) recovered 32 endophytic fungi collected from the rhizomes of six Zingiberaceae plants in central Java, Indonesia. The antioxidant activity of the fungal extracts was determined through the DPPH assay and their antibacterial effects were tested against *Escherichia coli* and *Staphylococcus aureus* using non-eluted TLC bioautography. Out of all the tested samples, 19 extracts demonstrated antioxidant effects. Moreover, an endophytic fungus known as *Fusarium oxysporum* was isolated from the rhizomes of *Z. zerumbet*, a medicinal plant endemic to North-East India. The extracts were evaluated for their DPPH free radical scavenging activity, total phenolic content, flavonoid content and COX inhibition assay. Among the studied extracts, Zfe 3 (hexane) displayed the highest DPPH radical scavenging activity (IC_{50}: 41.68 µg) (Nongalleima *et al*., 2013). Additionally, Vo *et al*. (2016) isolated *Aspergillus terreus, Streptomyces* sp., *Cladosporium* sp. and *Penicillium* sp. from galangal, ginger and laurel. Antioxidant activity testing using DPPH showed R-TN3 with the highest activity (62.32%), while T-TG3 had the lowest (30.95%) activity. The study by Taechowisan *et al*. (2017) explained that *Streptomyces* sp. strain BO-07, isolated from *Boesenbergia rotunda* root, yielded two biphenyl compounds: 3'-hydroxy-5-methoxy-3,4-methylenedioxybiphenyl and 3'-hydroxy-5,52 -dimethoxy-3,4-methylenedioxybiphenyl. Strong antibacterial properties were observed for both compounds against *Staphylococcus aureus*, *Bacillus cereus* and *Bacillus subtilis* (MIC: 0.5 µg/ml, MBC: 2-8 µg/ml), with high antioxidant activity (SC: 85.84-88.26 µg/ml). Furthermore, they isolated K3, K2 and M1b from *C. longa* showed antibacterial activity against *Salmonella entericaser*, *Staphylococcus aureus* and *Candida albicans*. Isolate K3 (*Paenibacillus alvei*) had the strongest antioxidant and strong antimicrobial activity against Gram-positive bacteria, whereas isolate K2 (*Enterobacter agglomerans*) demonstrated strong antimicrobial activity against Gram-negative bacteria, also exhibiting high antioxidant activity (Sulistiyani *et al*., 2016). Whereas, Hapsari *et al.* (2024) examined the antioxidant capacity of the turmeric endophytic fungus BoCiClD-2. After fermentation and purification, the extract exhibited high antioxidant activity, with subfraction II.2 being the most active (51.85%). The major molecule identified by NMR analysis was 3-hydroxy-4-methylbenzoic acid, indicating that BoCiClD-2 is a potential natural antioxidant source. In addition to this, the antioxidant activity of endophytic fungi like Cl. Bn1, Cl. Bn2 and Cl. Bn3 isolated from turmeric flowers was investigated using the DPPH technique. Both single and mixed fungal cultures exhibited antioxidant characteristics, with mixed cultures having higher activity. This is the first study to demonstrate the potential of a coupled endophytic fungus from turmeric blossoms as a natural antioxidant source (Septiana *et al*., 2020).

7. Commercialization of endophytic bioformulations

According to Blake *et al*. (2021), the multiple beneficial features of *B. velezensis* strains F18, HC-5 and L73 make them promising options for commercial formulation, offering a practical solution for managing ginger bacterial wilt (*Ralstonia solanacearum*) in agriculture. In the same way, Gupta *et al*. (2022) said that *Colletotrichum gloeosporioides* causes leaf spot in ginger, causing economic losses. Moreover, fungal endophytes like *Aspergillus terreus* can act as biocontrol agents because they live in the same areas as the harmful fungi. The study found *A. terreus* among many isolates, producing terrein, a compound with antibacterial, antifungal and anticancer effects. Likewise, these results suggest *A. terreus* has potential for commercial use in agriculture and medicine. On top of that, Marwan *et al*. (2023) developed a commercial biofungicide formulation to control rhizome rot disease in red ginger, caused by *Fusarium oxysporum*. The formulation includes *Trichoderma* sp. (TBP1) and *Bacillus* sp. (PBC 25 and PBC32), which inhibited pathogen growth by 83%, 53.3% and 50%, respectively, *in vitro*. When applied before planting and 30 days after planting, the formulation significantly reduced disease incidence (78.57-93.3%) and promoted plant growth. This commercial product offers an eco-friendly alternative for managing rhizome rot in red ginger. Similarly, Vinayarani and Prakash, (2018) reported that *Trichoderma harzianum* TharDOB-31 from turmeric rhizomes showed plant growth-promoting and biocontrol traits. Greenhouse trials demonstrated its effectiveness in reducing rhizome rot and leaf blight, boosting yield compared to chemical treatments. Microscopy confirmed colonization and its metabolites exhibited antimicrobial activity. These findings support its potential for commercial formulation as a biocontrol agent in turmeric cultivation.

8. Conclusion

Endophytes associated with the Zingiberaceae family represent a valuable and largely untapped resource with broad applications in agriculture, biotechnology and medicine. These symbiotic microorganisms contribute significantly to plant health by enhancing growth, improving nutrient uptake and offering natural protection against a range of pathogens. Their capacity to produce a diverse array of bioactive compounds, including antimicrobial, antifungal, antioxidant, anticancer and anti-inflammatory activity, further underscores their potential in replacing or supplementing conventional agrochemicals and pharmaceuticals. The integration of endophytes into spice crop cultivation systems, particularly in turmeric, ginger and cardamom, offers an eco-friendly and sustainable strategy for enhancing crop resilience and productivity while minimizing environmental impact. Additionally, their involvement in key plant growth-promoting activities such as phosphorus solubilization, nitrogen assimilation, siderophore production and phytohormone synthesis positions them as essential partners in the development of more sustainable agricultural practices. Advancements in omics technologies, molecular biology and genetic engineering now provide the tools necessary to explore the full metabolic and functional potential of Zingiberaceae-associated endophytes. Future research should be focused on isolating novel strains, characterizing their functional traits and evaluating their field-level effectiveness in different agro-climatic conditions. Understanding the molecular mechanisms underlying endophyte-host interactions will also pave the way for designing targeted bioinoculants and biocontrol agents. In conclusion, a multidisciplinary approach that combines traditional knowledge with modern scientific tools is essential to harness the full benefits of endophytes in the Zingiberaceae family. This will not only support the sustainable production of spice crops but also contribute to the discovery of new therapeutic agents, aligning agricultural practices with global goals for health and environmental sustainability.

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Abbreviation

TLC - Thin Layer Chromatography

NEH - North Eastern Hill

MIC - Minimum Inhibitory Concentration

GC-MS - Gas Chromatography-Mass Spectrometry

ITS - Internal Transcribed Spacer

COX - Cyclooxygenase

ROS - Reactive Oxygen Species

DPPH - 2,2-diphenyl-1-picrylhydrazyl

Conflict of interest

The author declares no conflicts of interest relevant to this article

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