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Endophytic Microorganisms and Bioactive Metabolites of *Avicennia marina*: A Natural Treasure for Biotechnology and Medicine

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The grey mangrove (*Avicennia marina*) hosts a varied array of endophytic microorganisms, which are crucial to the plant's adaptation in extreme coastal environments. These endophytes comprising bacteria and fungi play a crucial role in enhancing the host's stress tolerance, disease resistance, and nutrient cycling. In this way, they support the ecological resilience and productivity of mangrove ecosystems. Recent studies have shown that endophytes derived from *A. marina* produce a wide variety of bioactive metabolites—including alkaloids, flavonoids, terpenoids, phenolics, and various enzymes that possess strong antioxidant, antimicrobial, anticancer, insecticidal activities, as well as bioremediation properties. These compounds are highly promising for use in drug discovery, environmental remediation, and industrial biotechnology. Even with these advancements, challenges persist, such as cultivation difficulties, limited genomic insights, and scalability issues for practical applications. To fully realize the biotechnological and medicinal potential of *A. marina* endophytes, future efforts in this field should focus on integrating omics technologies and synthetic biology and investigating novel microbial taxa. This review highlights the ecological importance, metabolic diversity, and potential applications of endophytic microorganisms associated with *A. marina*, stressing their worth as a natural resource for sustainable innovation in biotechnology and medicine.

Keywords: ***Endophytic microorganisms, Avicennia marina, Mangrove endophytes, Bioactive metabolites, Secondary metabolites, Antioxidants, Bioremediation, Drug discovery, Biotechnology***

INTRODUCTION

Mangrove ecosystems, characterized by saline-tolerant shrublands and forests, serve as vital intertidal habitats that provide essential ecological services, including carbon sequestration, coastal protection, and marine biodiversity support. Among these, *Avicennia marina* (the grey mangrove) emerges as one of the most geographically widespread species, with a distribution spanning from Africa's western coasts to Indo-Pacific regions (Haseeba et al., 2025). This species plays a particularly significant role in maintaining these fragile ecosystems due to its exceptional adaptability to challenging intertidal conditions (Abdellatif and Arafat, 2024; Sukenda, 2019). Mangrove ecosystems, known for their saline coastal habitats, are among the most crucial intertidal environments worldwide. These ecosystems are essential due to their unique biodiversity and the vital ecosystem services they provide, serving as nursery habitats for marine life (Abdellatif and Arafat, 2024). *Avicennia marina* is renowned for its exceptional capacity to endure extreme environmental conditions, including high salinity, anoxic soils, heavy metal contamination, and varying tidal regimes (Masoud et al., 2019). The plant's physiological adaptations and its symbiotic relationships with endophytic microorganisms both contribute to this resilience (Al Husnain et al., 2023).

The extreme salinity, temperature fluctuations, and tidal conditions of mangrove ecosystems make them unique subjects for studying coastal resilience (Mohanty et al., 2024). *Avicennia marina* (grey mangrove) thrives in these harsh environments, partly due to symbiotic relationships with endophytic bacteria microorganisms that colonize internal plant tissues without causing harm (Abdellatif and Arafat, 2024). These endophytes enhance host survival by improving stress tolerance, nutrient acquisition, and pathogen resistance, making them valuable for biotechnological and agricultural applications (Sadeer et al., 2023, Alghamdi et al., 2024). Despite their ecological and biotechnological significance, the microbial communities associated with *A. marina* remain understudied. Recent reviews emphasize the limited exploration of mangrove-associated microbiomes, particularly in *A. marina*, underscoring the need for further research into this untapped microbial diversity.

Endophytes are microorganisms that reside within plant tissues without causing harm, often conferring benefits such as enhanced growth, stress tolerance, and disease resistance (Ali et al., 2017). In *A. marina*, endophytic communities have been isolated from various tissues, including leaves, roots, seeds, and pneumatophores, underscoring their ubiquity and ecological significance (Abdellatif and Arafat, 2024, Sukenda, 2019, Savitri et al., 2023). Recent studies have identified a broad spectrum of endophytic bacteria-such as *Bacillus*, *Mixta*, and *Cytobacillus* and fungi inhabiting *A. marina*, highlighting the plant's role as a reservoir of microbial diversity (Khalil et al., 2021).

The study aimed to critically synthesize and analyze the existing knowledge about endophytic microorganisms linked to *Avicennia marina* and the bioactive metabolites they generate. This review aims to underscore the ecological importance and diversity of these endophytes, provide a summary of recent discoveries regarding their biotechnological and antimicrobial potential, and examine the ramifications for medical practice, environmental stewardship, and forthcoming research endeavours. This article aims to serve as a thorough resource for researchers and practitioners looking to tap into the natural biotechnological and medicinal potential of *A. marina* and its microbial communities by consolidating evidence from recent studies.

2. *Avicennia marina*

Avicennia marina (Forssk.) Vierh., commonly known as the grey mangrove, is a keystone species with a circumglobal distribution, enabled by both hypochlorous (water) and anemochorous (wind) seed dispersal. This ecologically significant mangrove exhibits notable habitat-based variation and is currently classified into three allopatric varieties: *A. marina* var. *australasica*, var. *eucalyptifolia*, and var. *marina* (Asaf et al., 2021).

Mangrove ecosystems comprise approximately 70 species across 27 genera, 20 families, and 9 orders, found in 112 countries and covering about 25% of the world's coastlines estimated area of 180,000 km² (Jiang et al., 2018). *Avicennia marina* typically grows as a shrub or small tree, reaching 3 to 10 meters in height, but can grow up to 14 meters in tropical climates. It thrives in saline, intertidal zones of protected coastlines and is highly tolerant of harsh weather, including strong winds (Bobbarala et al., 2009, Chandrakala, 2019).

Taxonomically, *A. marina* belongs to the plant kingdom (Plantae), within the phylum Tracheophyta (vascular plants), class Spermatopsida (seed-bearing plants), order Lamiales, and family Acanthaceae. The genus *Avicennia* is well known for its adaptations to saline coastal habitats, with *A. marina* being one of the most widely distributed and ecologically important species in the group (Chan, 1992, Dahdouh-Guebas, 2025).

Morphologically, *A. marina* is characterized by a gnarled arrangement of multiple branches, smooth light-grey bark with thin, brittle flakes, and thick, glossy green leaves with silvery-white undersides (Figure 1). Specialized aerial roots called pneumatophores, which can reach up to 20 cm in height, allow the plant to absorb oxygen in waterlogged, anoxic soils. The leaves possess salt-excreting glands, enabling the tree to survive in high-salinity environments (Sasomsaptawee et al., 2015).

3. Diversity of Endophytic Microbiome in *Avicennia marina*

Avicennia marina (grey mangrove) harbours a highly diverse community of endophytic bacteria and fungi, which reside within its tissues without causing damage (Al Husnain et al., 2023, Abdellatif and Arafat, 2024). These endophytes are essential for supporting the plant's health, enhancing its resilience, and aiding its adaptation to challenging coastal conditions. Isolation of endophytic fungi from *Avicennia marina* leaf segments using selective culture media (Figure 2).

3.1 Bacterial Endophytes

Avicennia marina hosts a rich diversity of endophytic bacteria, colonizing its leaves, roots, seeds, and pneumatophores. Both culture-based and high-throughput sequencing approaches have identified Proteobacteria as the dominant phylum, along with significant representation from *Bacillaceae*, Enterobacteriaceae, and other bacterial families (Alghamdi et al., 2024, Megala and Vasan, 2023).The study carried out by Alghamdi et al. (2024) identified a diverse collection of 256 bacterial strains isolated from various compartments of the *Avicennia marina* mangrove ecosystem, including bulk soil, rhizosphere, rhizoplane, roots, and leaves along the Red Sea coast.

Figure 1. Morphological Progression and Structural Details of *Avicennia marina* Leaves

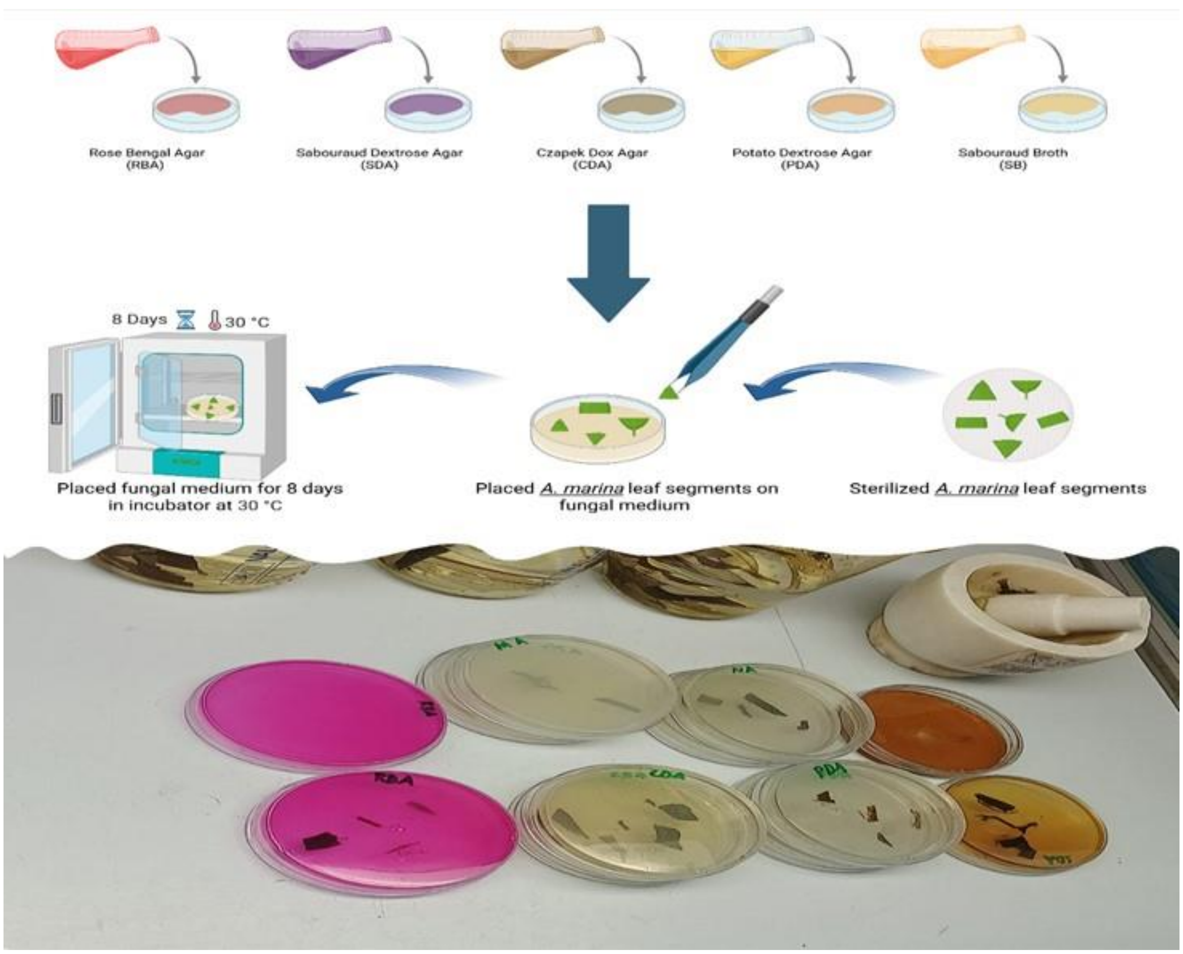

Figure 2. Stepwise procedure for culturing endophytic fungi from *Avicennia marina* on different agar media.

These isolates spanned 34 genera across four dominant phyla, with Proteobacteria being the most abundant (73.8%), followed by Firmicutes (17.2%), Actinobacteria (6.6%), and Bacteroidota (2.3%). Key genera included *Larsenimonas*, which dominated root samples (67%), *Halomonas* and *Vibrio* in the rhizosphere, and *Bacillus* in the rhizoplane (Alghamdi et al., 2024).

Another study identified two bacterial isolates from the mangrove leaves of *Avicennia marina* in Yanbu, Saudi Arabia: Mixta calida strain "Yanbu7" (OR762485) and Cytobacillus oceanisediminis strain "Yanbu2" (OR762486) (Abdellatif and Arafat, 2024).

Ali et al. (2017), isolated 28 endophytic bacterial strains from the leaves of the mangrove *Avicennia marina* in Oman. These isolates were identified through 16S rRNA sequencing and belonged to diverse genera, including *Bacillus* (8 strains, with *B. pumilus* AM11 being notable), *Lysinibacillus* (5 strains), *Halomonas* (3 strains), *Vibrio* (2 strains), *Paenibacillus* (1 strain), *Microbacterium* (1 strain), *Citrobacter* (1 strain), *Virgibacillus* (1 strain), *Exiguobacterium* (1 strain, *Exiguobacterium* sp. AM25), and an uncultured bacterium (1 strain). Among these, *Bacillus* and *Lysinibacillus* were the most dominant (Ali et al., 2017).

The study identified 18 bacterial species isolated from the mangrove leaves of *Avicennia marina*, which belong to the Gammaproteobacteria, Firmicutes, and Enterobacteria groups (Sukenda, 2019). The species include *Virgibacillus salexigens* strain JCM 30552, *Klebsiella* sp. TG-1, *Pantoea agglomerans* strain T2, *Vibrio tritonius* strain AM2, *Vibrio* sp. MSSRF QS47, *Enterobacter asburiae* strain idli 48, *Staphylococcus saprophyticus* strain GRKJM1, *Pseudomonas* sp. R-9, *Vibrio natriegens* strain ATCC 14048, *Enterobacter* sp. 1FTM7, *Bacillus subtilis* strain BR4, *Bacillus megaterium* strain YC4-R4, *Bacillus firmus* strain PGRP4, *Bacillus thuringiensis* strain VKK-SL-2, *Bacillus subterraneus* strain FJAT-47744, *Bacillus vietnamensis* strain FJAT-46928, *Bacillus* sp. strain FJAT 47851, and *Bacillus circulans* strain MD1. Among these, *Vibrio* sp. MSSRF QS47, *Pseudomonas* sp. R-9, and *Bacillus subtilis* strain BR4 exhibited the strongest inhibitory effects against *Stenotrophomonas maltophilia*, the causative agent of ice-ice disease in seaweed. These findings highlight the potential of mangrove-associated endophytic bacteria as biocontrol agents in aquaculture (Sukenda, 2019).

The fermentation liquid of *Avicennia marina* mangrove leaves contained eight identified *Bacillus* species: *Bacillus subtilis* MSAR-01, *Bacillus megaterium* MSAR-02, *Bacillus firmus* MSAR-03, *Bacillus thuringiensis* MSAR-04, *Bacillus subterraneus* MSAR-05, *Bacillus vietnamensis* MSAR-06, *Bacillus* sp. MSAR-07, and *Bacillus circulans* MSAR-08. Among these, are *B. subtilis* MSAR-01, *B. vietnamensis* MSAR-06, and *Bacillus* sp. MSAR-07 demonstrated the strongest inhibitory effects against *Stenotrophomonas maltophilia*, the pathogen responsible for ice-ice disease in seaweed (Rahman and Ekasari, 2020).

The study isolated 13 bacterial strains from the pneumatophores of *Avicennia marina*, with four key strains identified: *Bacillus* sp. (SjAM16101), *Enterobacter* sp. (SjAM16102), *Sporosarcina aquimarina* (SjAM16103), and *Bacillus cereus* (SjAM16104) (Janarthine and Eganathan, 2012). The study identified three bacterial endophytes isolated from the leaf tissues of *Avicennia marina* in the Kebun Raya Mangrove Surabaya, East Java, Indonesia. These isolates are characterized as *Bacillus subtilis* YRL02 (Isolate A), *Bacillus subtilis* HYM07 (Isolate B), and *Bacillus* sp (Savitri and Askitosari, 2024).

The mangrove ecosystem harbours diverse endophytic bacteria with significant ecological and biotechnological potential. Among these, a novel species, *Jiella avicenniae* sp. nov., was recently identified as an endophytic bacterium isolated from the bark of *Avicennia marina*. This discovery adds to the growing catalogue of microbial diversity associated with mangrove plants and highlights their untapped potential for plant growth promotion and environmental applications (Zhang et al., 2022).

3.2 Fungal Endophytes

Endophytic fungi associated with *Avicennia marina* (grey mangrove) display remarkable diversity and play important ecological and biomedical roles. Studies have isolated a wide range of fungal genera from *A. marina* tissues, including *Chaetomium*, *Aspergillus*, *Alternaria*, *Curvularia*, and *Penicillium* among others(Bharathidasan and Panneerselvam, 2011, Khalil et al., 2021) (Figure 3). These endophytes thrive in the harsh, saline, and sometimes heavy metal-contaminated environments where *A. marina* grows, and many produce bioactive metabolites with antimicrobial and antioxidant properties (Khalil et al., 2021). For example, from *A. marina* leaves, 12 fungal species were isolated, with *Aspergillus niger*, *Penicillium rubens*, and *Alternaria alternata* being the most prevalent (isolation frequency: 80%; relative density: 12.5%) (Table 1). Other species, such as *Exserohilum rostratum* and *Mucor racemosus*, showed lower frequencies. These findings align with global studies reporting *Penicillium* and *Aspergillus* as dominant genera in mangrove ecosystems due to their adaptability and metabolic versatility (Al-Rajhi et al., 2022).

3.3 Factors Influencing Microbial Diversity

The diversity of endophytic microbial communities in *Avicennia marina* mangrove ecosystems is affected by various factors. Environmental factors like i) salinity, ii) temperature, and iii) heavy metal contamination are crucial, as *A. marina* flourishes in extreme coastal environments where these stressors are common. Resilient endophytes that can tolerate or thrive under high salt and metal concentrations are selected for these severe conditions, resulting in unique and potentially advantageous microbial assemblages (Abdellatif and Arafat, 2024, Khalil et al., 2021).

The diversity of endophytes is also influenced by geographical location and the ecological characteristics of the region.

Table 1. Diversity and frequency of endophytic fungi isolated from leaves of *Avicennia marina* across different regions

Region	Plant part	Endophytic fungi	Isolation frequency (%)	Relative density (%)	References
Jazan (Saudi Arabia)	Leaf	*Aspergillus niger,*	(80%)	(12.5%)	(Al-Rajhi et al., 2022)
		Alternaria alternata	(80%)	(12.5%)	
		Exserohilum rostratum	(60%)	(10%)	
		Mucor racemosus	(40%)	(5%)	
		Acremonium sp.	(20%)	(3.12%)	
		Penicillium rubens	(80%)	(12.5%)	
		Alternaria chlamydospore	(60%)	(10%)	
		Fusarium proliferatum	(60%)	(10%)	
		Aspergillus phoenicis	(40%)	(5%)	
		Penicillium chrysogenum	(60%)	(10%)	
		Cladosporium herbarum	(60%)	(10%)	
		Eurotium amstelodam	(20%)	(3.12%)	
Tarut Island (between Jeddah and Jazan, Saudi Arabia)	Leaf	*Paecilomyces variotii*	-	-	(Basheer et al., 2018)
		Chaetomium globosum	-	-	
		Aspergillus niger	-	-	
		Penicillium chrysogenum	-	-	
		Penicillium charlesii	-	-	
		Talaromyces minioluteus	-	-	
		Aspergillus oryzae	-	-	
		Paecilomyces maximus	-	-	
Abu Hamrah stand and South Safaga stand (Egypt)	Leaf	*Aspergillus aculeatus*	(50%)	(8.57%)	(S Metwally et al., 2020)
		Eurotium amstelodami	(21.43%)	(5.71%)	
		Aspergillus niger	(60.71%)	(5.71%)	
		Mucor racemosus	(3.57%)	(2.85%)	
		Aspergillus phoenicis	(60.71%)	(2.85%)	
Yanbu (Saudi Arabia)	Leaf	*Aspergillus hiratsukae*	-	-	(Khalil et al., 2021)
		Alternaria tenuissima	-	-	
		Chaetomium sp.	-	-	
		Chaetomium madrasense	-	-	
		Curvularia lunata	-	-	
		Aspergillus ochraceus	-	-	
		Chaetomium globosum			

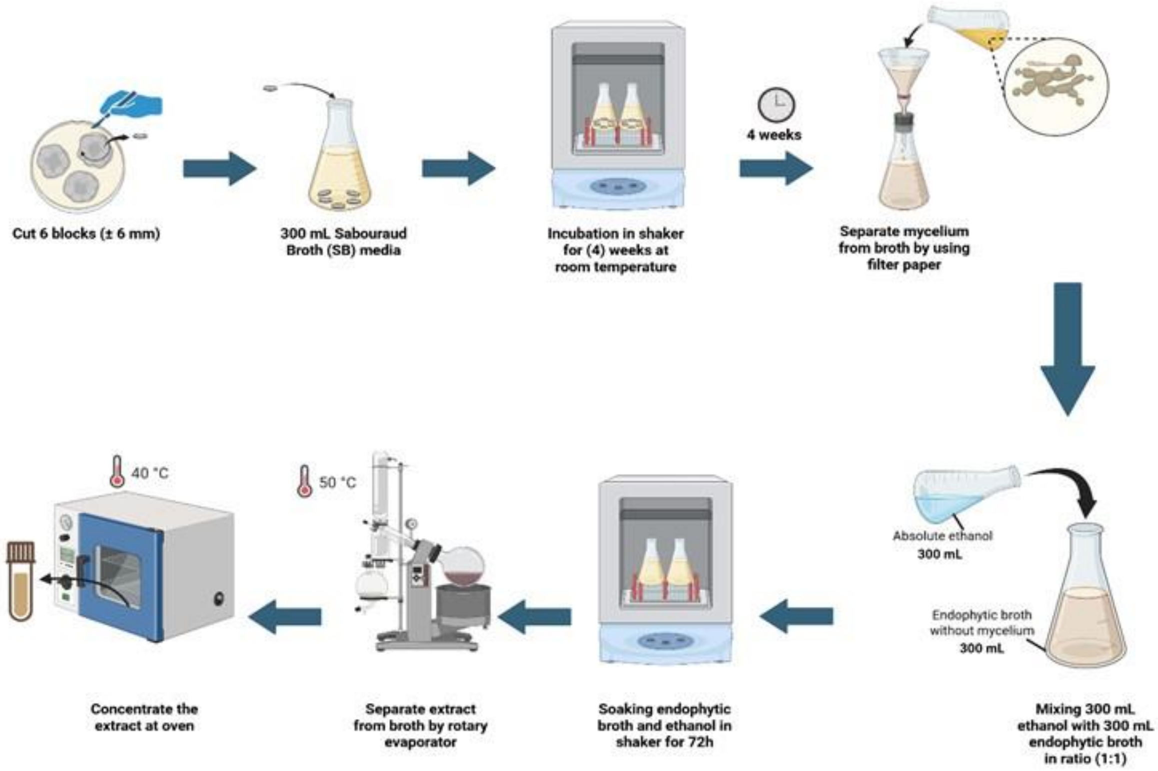

Figure 3. Workflow for the extraction of bioactive metabolites from endophytic fungi using the ethanol-sabouraud broth method.

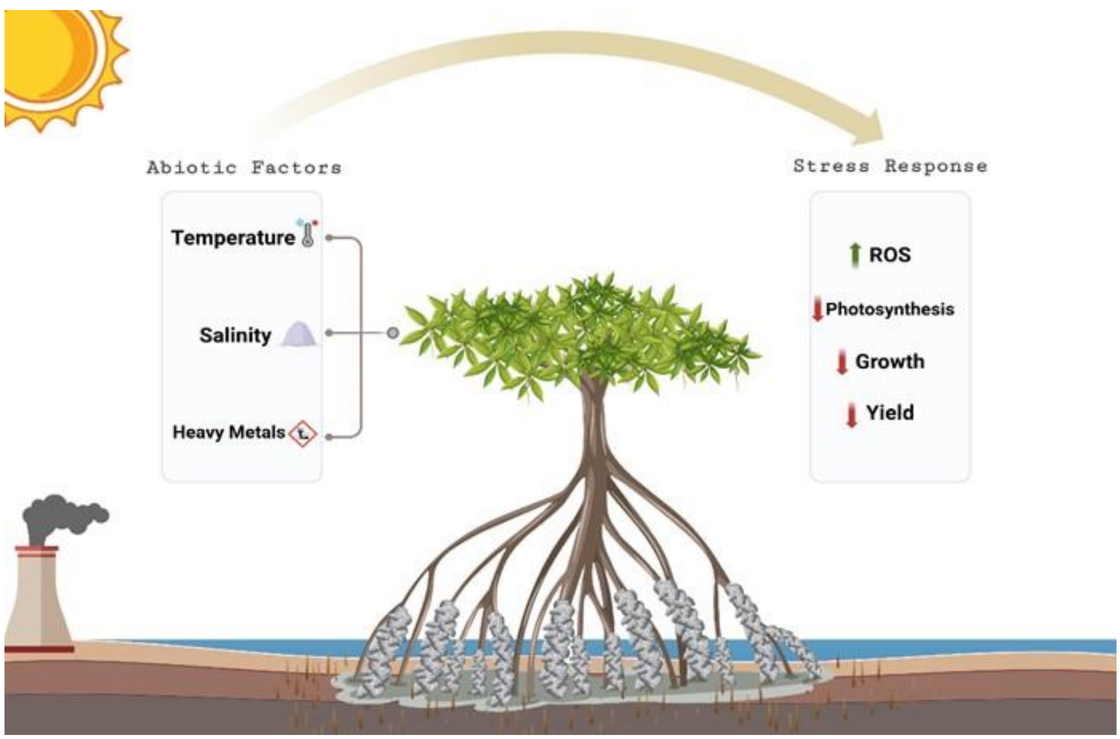

Figure 4. Schematic representation of abiotic stress and physiological responses in mangrove plants

The plant's biochemical characteristics, including the generation of tannins and other metabolites, can influence which microbes are able to successfully colonize its internal tissues (Costa et al., 2012). Overall, these influences produce a multifaceted, dynamic environment in which the endophytic microbial diversity of *A. marina* mangroves is formed by both abiotic and biotic factors, thereby playing a role in the ecological resilience and biotechnological potential of these mangroves (Figure 4).

Research comparing various locations, including those along the Red Sea coast and other areas rich in mangroves, has discovered that local environmental factors and the health of plants can lead to unique microbial communities within *A. marina*.

Moreover, the sampled part of the plant (such as roots, stems, leaves, or fruits) affects the diversity and composition of endophytes. Roots usually exhibit the greatest genus diversity, followed by stems and fruits (Abdellatif and Arafat, 2024, Noviyanto, 2025). The structure of the endophytic community is also influenced by seasonal variation, plant age, and developmental stage, as well as by human-induced factors such as pollution and habitat disturbance.

4. Bioactive Metabolites

4.1 Types of Bioactive Metabolites

Avicennia marina has been extensively studied for its rich phytochemical composition, with various classes of bioactive compounds identified in different plant parts, including leaves, bark, seeds, and aerial roots (Figure 5). Phytochemical analyses reveal the presence of alkaloids, flavonoids, glycosides, phenols, saponins, steroids, tannins, and terpenoids, as documented across multiple studies (Govindhan, 2024). Notably, flavonoids such as luteolin derivatives, quercetin, and kaempferol have been isolated from leaves and seeds, while naphthalene derivatives like avicennones and avicequinones exhibit significant bioactivity (Zhou et al., 2025). Steroids, including β-sitosterol and stigmasterol derivatives, along with terpenoids such as betulinic acid and ursolic acid, contribute to the plant's pharmacological potential (ElDohaji et al., 2020). Additionally, fatty acids like oleic and linolenic acids demonstrate antimicrobial properties (Al-Mur, 2021), while glucosides such as verbascoside and marinoids show therapeutic promise (Zhou et al., 2025). Pharmacological studies highlight the medicinal value of these compounds, with avicennones C, E, and F displaying antiproliferative and antimicrobial effects, and stenocarpoquinone B exhibiting anticancer potential (Han et al., 2007). Betulinic acid is recognized for its anticancer and anti-inflammatory properties (ElDohaji et al., 2020), while stigmasterol-3-O-β-D-glucopyranoside shows antiglycation activity (Mahera et al., 2013).

4.2 Antimicrobial Compounds

Avicennia marina has demonstrated significant antimicrobial potential through various bioactive compounds isolated from different plant parts (Figure 6). Naphthalene derivatives, particularly avicennones C, E, and F (compounds) and stenocarpoquinone B (30) exhibit strong antimicrobial properties against bacterial and fungal pathogens (Bournot, 1913). Additionally, avicennone G and avicequinone C contribute to the plant's antimicrobial defense mechanisms (Bournot, 1913, Manilal et al., 2009). The antimicrobial effects extend to fatty acid constituents, including oleic acid, linolenic acid, palmitic acid, stearic acid, lauric acid, and myristic acid, which likely act by disrupting microbial cell membranes (Manilal et al., 2009, Farag et al., 2021). Furthermore, 9-octadecenamide has shown promising antimicrobial activity (Ulqodry et al., 2023). These findings position *A. marina* as a valuable source of natural antimicrobial agents with potential applications in addressing antibiotic resistance. However, further research is needed to fully characterize these compounds' mechanisms of action and therapeutic potential. The diverse array of antimicrobial phytochemicals in *A. marina* underscores its importance in traditional medicine and highlights its potential for developing novel antimicrobial drugs.

4.3 Anticancer Agents

Avicennia marina has emerged as a promising source of natural anticancer compounds, with several of its phytochemicals demonstrating significant antiproliferative and cytotoxic activities against various cancer cell lines (Figure 7). Among the most notable anticancer agents identified are the naphthalene derivatives, particularly avicennone C and stenocarpoquinone B, which have shown potent antiproliferative effects (Bournot, 1913). The triterpenoid betulinic acid stands out as a particularly valuable compound, exhibiting well-documented anticancer activity through multiple mechanisms including induction of apoptosis and anti-inflammatory effects (Han et al., 2008, Hossain et al., 2012, Zhu et al., 2009).

The plant's steroid constituents, especially stigmasterol-3-O-β-D-glucopyranoside , have demonstrated antiglycation properties that may contribute to their anticancer potential (Han et al., 2008). Additionally, several abietane-type diterpenoids, including compounds (6Hα-11,12,16-trihydroxy-6,7-secoabieta-8,11,13-triene-6,7-dial 11,6-hemiacetal) and (6,11,12,16-tetrahydroxy-5,8,11,13-abitetetraen-7-one), have shown promising anticancer activities (Singh et al., 2013). The presence of these diverse anticancer compounds in different plant parts suggests that *A. marina* could serve as a rich source for developing novel chemotherapeutic agents or adjuvants.

4.4 Antioxidants for Health Applications

Antioxidants sourced from both endophytic fungi and plant extracts of *Avicennia marina* have shown considerable promise in counteracting free radicals and shielding biological systems from oxidative stress (Figure 5). Research has demonstrated that endophytic fungi extracted from different parts of *A. marina*, such as roots, stems, and fruits, generate a range of phenolic compounds recognized for their antioxidant properties (Khalil et al., 2021, Noviyanto, 2025). For example, extracts from endophytic fungi like *Neopestalotiopsis* sp. and *Aspergillus niger* (obtained from the fruit) demonstrated exceptionally strong antioxidant activity, as evidenced by IC_{50} values under 20 µg/mL, which signifies high potency. Numerous bioactive antioxidant compounds, including phenolics, terpenoids, and saponins, have been confirmed to be present in these fungal extracts through gas chromatography-mass spectrometry (GC-MS) analyses (Noviyanto, 2025, Khalil et al., 2021, Yoswaty et al., 2023). The research carried out by Alrubaye (2024) involved a thorough investigation of the antioxidant mechanisms of mangrove extracts, bringing to light the existence of various essential bioactive compounds that are accountable for these effects (Figure 8).

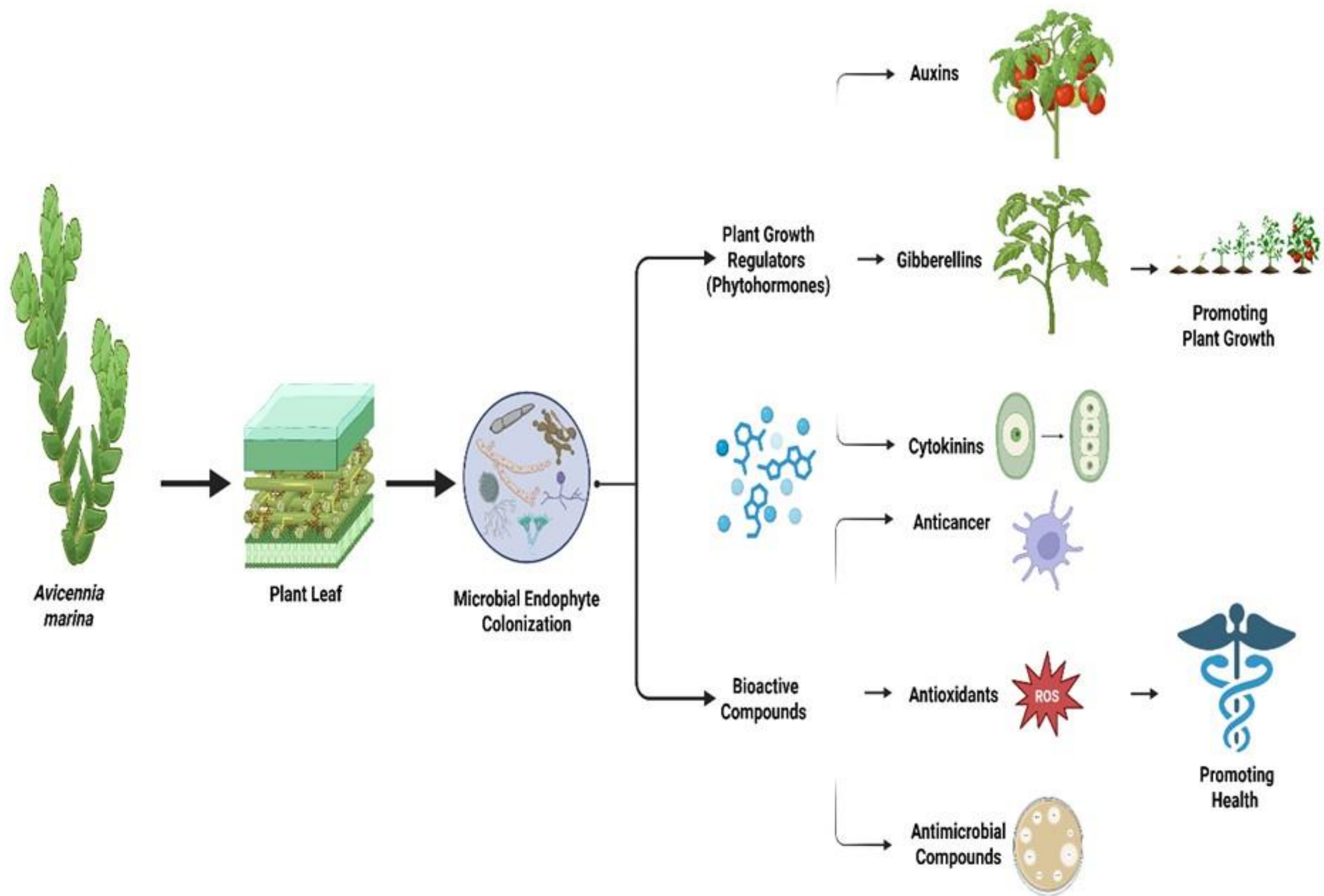

Figure 5. Schematic overview of bioactive compound production by endophytes in *Avicennia marina*

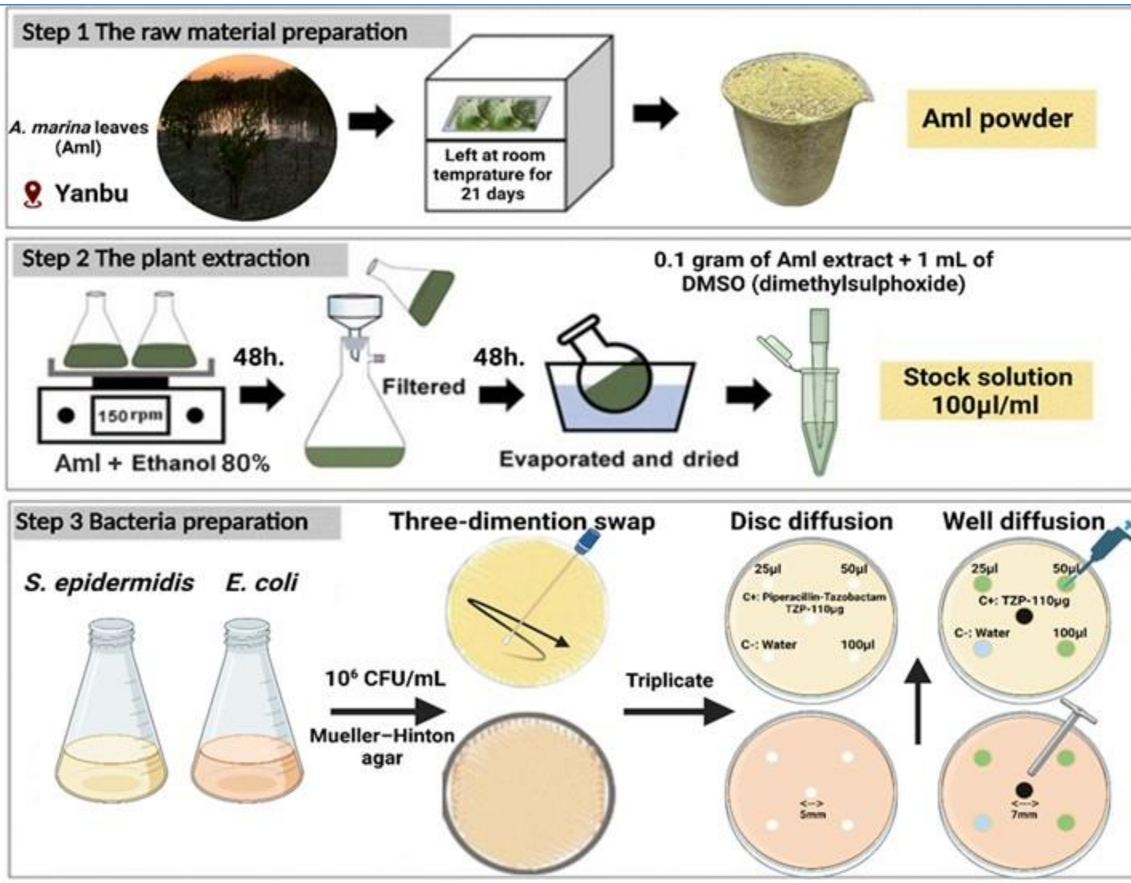

Figure 6. Schematic representation of plant extraction and antimicrobial assay procedures using *Avicennia marina* leaves

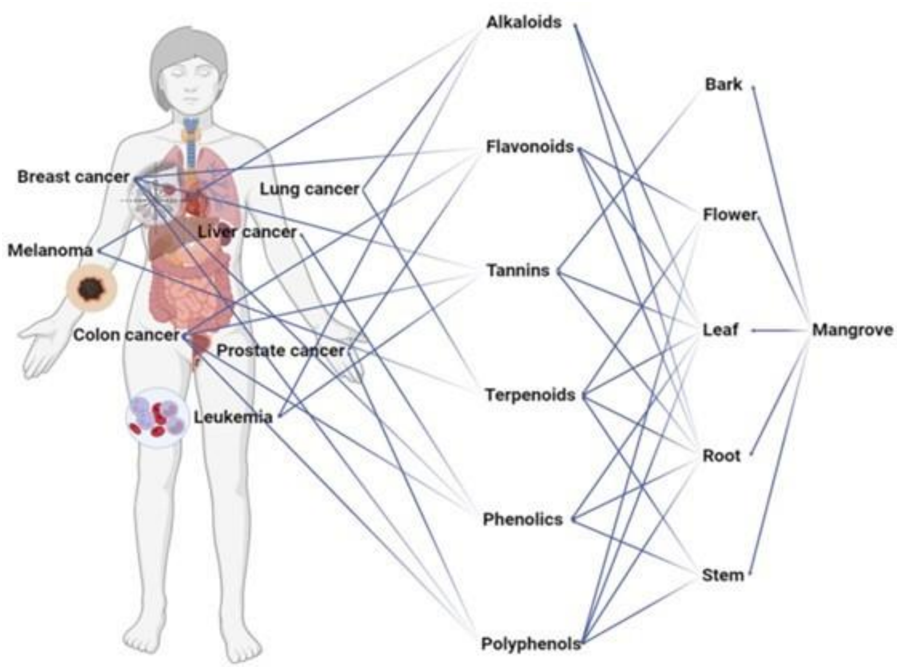

Figure 7. Approaches in which mangrove extracts act against cancer. This illustration emphasizes essential elements like the bioactive compounds found in mangrove extracts and their relationships with cancer cells, which result in a range of anticancer effects (Alrubaye et al., 2024).

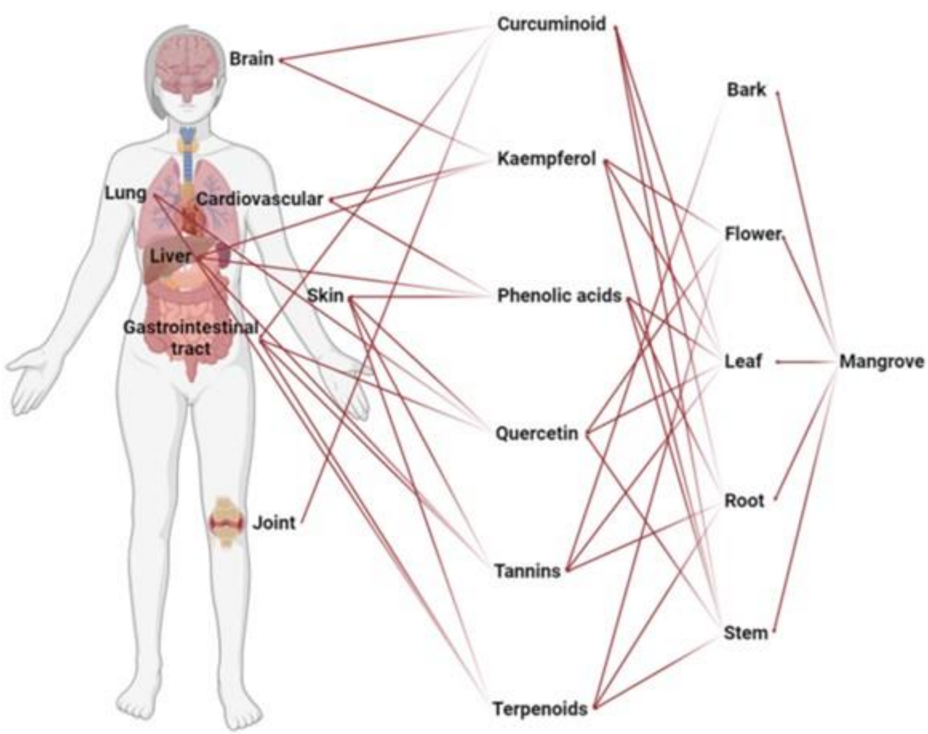

Figure 8. Mechanisms of antioxidant and anti-inflammatory activities of mangrove extracts (Alrubaye et al., 2024).

The compounds like curcuminoids, kaempferol, phenolic acids, quercetin, tannins, and terpenoids mainly sourced from different parts of the mangrove plant such as leaves, bark, flowers, roots, and stems—were recognized as strong antioxidants. These substances help lessen oxidative stress by counteracting free radicals and bolstering cellular protection mechanisms. These phytochemicals demonstrated antioxidant activity that provided protective effects for various organs, especially the brain, liver, cardiovascular system, skin, and gastrointestinal tract (Alrubaye et al., 2024). Khalil's (2021) investigation demonstrated that endophytic fungi obtained from *Avicennia marina* leaves showed significant antioxidant activity. Isolated from a severe, heavy metal-tainted mangrove environment, these fungi were discovered to generate numerous phenolic compounds recognized for their potent antioxidant characteristics.

Alongside their low cytotoxicity against the ATCC-CCL-81 cell line, the extracts demonstrated antioxidant potential, indicating their safety and therapeutic relevance (Khalil et al., 2021). The results indicate that endophytic fungi from extreme environments such as mangroves may be promising natural sources of antioxidant compounds for potential use in pharmaceuticals.

4.5 Insecticidal activity

Insecticidal impacts have been observed in bioactive compounds extracted from *Avicennia marina* leaves using methanol, ethyl acetate, and hexane, specifically against test insects such as *Gryllus bimaculatus* and *Tenebrio molitor* (Figure 9). The methanol extract exhibited the highest mortality rates, with LC_{50} values suggesting moderate toxicity. Phytochemical examinations showed that organic fatty acids, alcohols, and esters were the main components. The overall insecticidal activity of *A. marina* extracts is classified as low and non-toxic; however, these findings indicate a potential for their development as eco-friendly bioinsecticides, particularly when used in conjunction with other pest management strategies (Ulqodry et al., 2023). Moreover, silver nanoparticles that were biosynthesized using *A. marina* leaf extract demonstrated strong larvicidal effects on mosquito larvae (*Aedes aegypti* and *Anopheles stephensi*), with LC_{50} values in the low mg/L range, thereby supporting their use in vector control initiatives (Balakrishnan et al., 2016).

4.6 Enzymes with Industrial Applications

The endophytic microorganisms associated with *Avicennia marina*, as well as the organism itself, are abundant in enzymes that have important uses in both industry and environmental environments. A remarkable enzyme extracted from *A. marina* is the novel Cu/Zn-superoxide dismutase (AmSOD), which demonstrates both high catalytic efficiency and exceptional stability over a wide range of pH and temperature conditions. Due to its ability to withstand denaturation, this enzyme is well-suited for various biotechnological and pharmacological applications, such as being included in antioxidant products and aiding in the creation of stress-tolerant crops (Zeinali et al., 2017, Rafiei and Shahpiri, 2025).

Catalase (AmCAT) is another vital enzyme discovered in *A. marina*, and it is essential for breaking down hydrogen peroxide and protecting cells from oxidative harm. AmCAT, when expressed heterologously in Escherichia coli, improved the bacteria’s tolerance to heavy metals, salinity, butanol, and oxidative stress. Such attributes underscore its promise in the fields of industrial biotechnology and bioremediation, where enzymes are required to operate effectively despite severe environmental conditions (Rafiei and Shahpiri, 2025).

Hydrolytic enzymes, including cellulase and phosphatase, are produced by endophytic bacteria isolated from the pneumatophores of *A. marina*, such as species from *Bacillus*, *Enterobacter*, and *Sporosarcina aquimarina*. These enzymes are useful in agriculture for enhancing nutrient availability and supporting plant growth, as well as in waste management and biomass conversion sectors. In addition, some endophytic actinobacteria, particularly *Streptomyces tubercidicus*, produce the enzymes ACC deaminase and nitrogenase. While nitrogenase promotes biological nitrogen fixation, aiding in soil fertility and sustainable farming, ACC deaminase reduces plant ethylene levels during stress to improve plant resilience (Alkaabi et al., 2022).

In addition to its agricultural applications, the biomass of *A. marina* is a potent green biosorbent for wastewater treatment, especially in the decolorization of textile dyes (Vaish and Pathak, 2024). The plant and its microbiome's enzymatic activities aid in the degradation of pollutants and heavy metals, thereby supporting eco-friendly bioremediation approaches. In conclusion, the various enzymes sourced from *Avicennia marina* and its endophytes show significant potential for use in biotechnology, environmental management, and sustainable farming practices (Rafiei and Shahpiri, 2025, Alkaabi et al., 2022).

5. Ecological Roles of Endophytes

In the grey mangrove (*Avicennia marina*), endophytes are crucial for improving the plant's survival, adaptation, and ecological performance in challenging coastal conditions. Bacteria and fungi are among these microorganisms, which help the mangrove’s resilience and ecosystem services through stress tolerance, nutrient cycling, bioremediation, and pathogen defense (Abdellatif and Arafat, 2024).

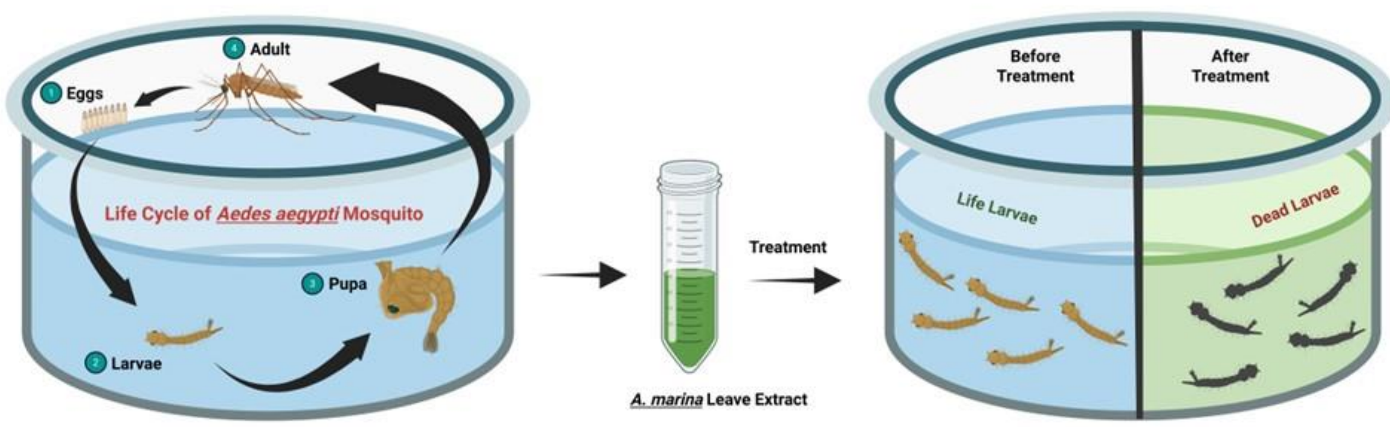

Figure 9. Schematic experimental illustration of *Aedes aegypti* larval mortality induced by *Avicennia marina* leaf extract

5.1 Stress Tolerance in Host Plants

Endophytes are crucial to the ecology of *Avicennia marina*, supporting the plant’s survival, strength, and ecological functions in difficult mangrove settings. Endophytes play a major role in improving stress tolerance in host plants. Mangrove ecosystems are characterized by unique environmental conditions like high salinity, the presence of heavy metals, and tidal fluctuations. These conditions promote the establishment of endophytic communities that assist their host in coping with abiotic stressors. As an illustration, it has been demonstrated that endophytic bacteria in *A. marina* can enhance plant growth and bolster resistance to salinity and heavy metals through the production of bioactive substances and the promotion of nutrient absorption. These microorganisms can accumulate or transform toxic metals, serving as natural biofilters and aiding the plant's adaptation to contaminated environments. Fungal endophytes aid in stress tolerance by generating secondary metabolites with antioxidant properties, thus providing additional protection against oxidative damage (Abdellatif and Arafat, 2024, Khalil et al., 2021, Alrubaye et al., 2024).

The study identified a diverse collection of 256 bacterial strains isolated from various compartments of the *Avicennia marina* mangrove ecosystem along the Red Sea coast. The isolates exhibited remarkable halotolerance, with 93% thriving in high salinity (up to 5 M NaCl) and 50% classified as extreme halophiles, along with thermotolerance, as 66.8% grew at 45°C. Functionally, many strains demonstrated plant growth-promoting traits, including siderophore production (84.8%), pectinase activity (85.2%), and indole-3-acetic acid (IAA) production (57%). Notably, five strains—*Bacillus seohaeanensis* AK031, *Halobacillus locisalis* AK116, *Isoptericola* sp. AK164, *Tritonibacter mobilis* AK171, and *Pseudomonas azotoformans* AK225—significantly enhanced *Arabidopsis thaliana* growth under salt stress, increasing fresh weight by 20–165% compared to controls. These findings highlight the ecological significance of mangrove-associated bacteria and their potential applications as biofertilizers to improve crop resilience in saline soils or as bioremediation agents for degraded coastal ecosystems (Alghamdi et al., 2024).

Two strains, *B. pumilus* AM11 and *Exiguobacterium* sp. AM25, demonstrated exceptional tolerance to high salinity (5 M NaCl), making them promising candidates for enhancing plant resilience under salt stress. Phylogenetic analysis revealed 79–100% similarity to known bacterial sequences, with evolutionary relationships inferred using maximum parsimony and neighbor-joining methods. These endophytes significantly improved tomato plant growth under salinity stress by boosting biomass, photosynthetic efficiency, and antioxidant activity (e.g., catalase and peroxidase), while reducing oxidative damage. Their ability to stabilize ion imbalances highlights their potential as bioinoculants for crops in saline environments (Ali et al., 2017).

Among other studies, the isolates *S. aquimarina* SjAM16103—a Gram-variable, motile bacterium—exhibited notable plant growth-promoting traits, including indole acetic acid (IAA) production (2.37 μMol/mL), phosphate solubilization, nitrogen fixation, and siderophore secretion. Tolerant to 2–9% NaCl and optimal at 32°C and pH 7.0–9.0, SjAM16103 significantly enhanced root and shoot growth in inoculated plants (*Bacopa monnieri*, *Eupatorium triplinerve*, *Excoecaria agallocha*, and *A. marina*), demonstrating early root development and root hair formation. This marks the first report of endophytic *S. aquimarina* from *A. marina*, highlighting its potential as a biofertilizer for sustainable agriculture (Janarthine and Eganathan, 2012).

These isolates, characterized as *Bacillus subtilis* YRL02 (Isolate A), *Bacillus subtilis* HYM07 (Isolate B), and *Bacillus* sp. (Isolate C), were evaluated for their effects on plant growth and development. All three isolates, along with a control strain of *Bacillus subtilis* (Isolate K), demonstrated the ability to produce Indole Acetic Acid (IAA) and siderophores, indicating their potential roles in promoting plant growth and enhancing nutrient acquisition. Notably, *Bacillus subtilis* YRL02 and HYM07 significantly accelerated the transition of *A. marina* from the vegetative to the generative phase, with flowering observed in treated plants within just two weeks. While no significant changes in leaf dimensions were detected, the formation of infection zones around inoculation sites confirmed successful bacterial colonization. These findings underscore the potential of these endophytic bacteria to support mangrove rehabilitation and ecosystem restoration, particularly through their growth-promoting and stress-alleviating properties. Further research could explore their applications as biofertilizers or biocontrol agents in challenging environmental conditions (Savitri and Askitosari, 2024).Alongside a control strain of *Bacillus subtilis* (Isolate K), all three isolates demonstrated the ability to produce Indole Acetic Acid (IAA) and siderophores, key metabolites involved in plant growth promotion and nutrient acquisition. Notably, *Bacillus subtilis* YRL02 and HYM07 induced a rapid transition of *A. marina* from the vegetative to the generative phase, with flowering observed in treated plants within two weeks. Although no significant changes in leaf dimensions were detected, the formation of distinct infection zones around inoculation sites confirmed successful bacterial colonization. The discovery of *Jiella avicenniae* sp. nov. and the functional characterization of *Bacillus* isolates underscore the ecological importance of endophytic bacteria in mangrove ecosystems. These microbes exhibit promising traits for enhancing plant resilience, including stress tolerance and growth stimulation, making them potential candidates for mangrove rehabilitation and sustainable agricultural practices. Future research should explore the mechanistic basis of their plant-growth-promoting properties and their applications as biofertilizers or biocontrol agents in challenging environments (Zhang et al., 2022).

5.2 Disease Resistance

Along with being tolerant to stress, endophytes play a major role in the disease resistance of *A. marina*. Fungi that were isolated from endophytic sources in this species of mangrove have shown a significant capacity to oppose plant pathogens, including those that impact crops of economic significance like tomatoes. These fungi generate various bioactive metabolites that possess antimicrobial properties, hindering the growth of pathogenic bacteria and fungi. For example, extracts from the leaves of *A. marina* have demonstrated strong inhibitory effects on pathogens such as *Pseudomonas* *aeruginosa* and *Staphylococcus aureus*, highlighting the plant's promise as a source of natural antimicrobial agents. Diverse endophytic communities provide functional redundancy, bolstering the plant's resistance to diseases and environmental changes (Al Husnain et al., 2023, Khalil et al., 2021, Abdellatif and Arafat, 2024).

5.3 Nutrient Cycling

Endophytes play a crucial role in nutrient cycling in mangrove ecosystems. Several endophytic bacteria associated with *A. marina* can fix nitrogen, solubilize phosphate, and produce siderophores, which enhances nutrient availability in coastal soils that lack nutrients. These processes help *A. marina* grow and thrive, while also aiding the overall ecological functioning of mangrove habitats through organic matter decomposition and nutrient recycling. The endophytic microbes found in *A. marina* exhibit significant diversity and functional capabilities, underscoring their vital role in sustaining ecosystem services like carbon sequestration, bioremediation, and coastal protection (Abdellatif and Arafat, 2024, Alrubaye et al., 2024, Cherigo et al., 2024).

6. Challenges in Research

6.1 Cultivation Challenges

A key challenge is the cultivation of both the host plant and its endophytes. The tissue culture of *A. marina* is complicated due to problems like explant browning and the ongoing presence of endophytes, which can become pathogenic or provoke stress responses that result in tissue death. It is challenging to eliminate endophytes from explants, even with plant preservative mixtures and antioxidants, as these microbes can endure standard surface sterilization methods. They may also proliferate during in vitro culture, particularly in samples from contaminated environments where endophytes exhibit greater resistance to sterilants. Moreover, *A. marina* poses difficulties for propagation because of its recalcitrant seeds and particular environmental needs, which complicate laboratory cultivation and experimental manipulation (Savitri et al., 2024, Savitri and Askitosari, 2024).

6.2 Genomic Insights Needed

The necessity for more profound genomic insights represents a second challenge. Although research has started to describe the cultivable bacterial and fungal endophytes of *A. marina*, the complete diversity and functional capabilities of these communities are still insufficiently investigated, especially at the genomic level. Numerous endophytes cannot be cultivated using existing methods, and a comprehensive understanding of their functions in plant health, stress tolerance, and metabolite production requires advanced genomic and metagenomic techniques. This gap restricts our comprehension of endophyte-host interactions and the pinpointing of genes accountable for advantageous traits (Soldan et al., 2019, Khalil et al., 2021, Sukenda, 2019).

6.3 Scalability Issues

Another important issue is scalability. Even when promising endophytes or their metabolites are found, it is difficult to translate laboratory results into practical field applications or commercial production. Aspects like the necessity for particular growth conditions, challenges associated with the mass cultivation of endophytes, and the preservation of their advantageous characteristics outside their natural host environment complicate large-scale utilization. Furthermore, the variation in endophyte communities caused by environmental factors like pollution and location contributes to the complexity of standardizing applications and guaranteeing consistent outcomes (Savitri and Askitosari, 2024).

7. Future Directions

7.1 Integrating Omics Technologies

Future studies on endophytes in *Avicennia marina* will greatly benefit from the combination of advanced omics technologies, the use of synthetic biology, and exploration beyond currently known taxa. The integration of omics approaches, including genomics, transcriptomics, proteomics, and metabolomics, will yield comprehensive insights into the diversity, functional capabilities, and metabolic networks of endophytic communities. By uncovering the genetic underpinnings of characteristics such as stress tolerance, promotion of plant growth, and generation of bioactive metabolites, these technologies allow scientists to associate particular genes or pathways with advantageous phenotypes in both the host plant and its endophytes. For instance, metagenomic sequencing can reveal uncultivable or rare microbes and their biosynthetic gene clusters, while transcriptomic and metabolomic analyses can elucidate how endophytes respond to environmental cues or interact with *A. marina* at the molecular level (Savitri et al., 2023, Alkaabi et al., 2022).

7.2 Synthetic Biology Approaches

By utilizing synthetic biology, researchers can design endophytes or their metabolic pathways to augment beneficial characteristics or synthesize useful substances in large quantities. Researchers can enhance the production of plant growth regulators, stress-resistance factors, or novel pharmaceuticals by reconstructing biosynthetic pathways in model microbial hosts or directly editing endophytic genomes. Such approaches could facilitate the creation of synthetic microbial consortia customized for particular ecological or biotechnological purposes, like enhancing mangrove restoration initiatives or producing new pharmaceuticals from endophytic metabolites that were previously difficult to access (Alkaabi et al., 2022).

7.3 Expanding Exploration Beyond Known Taxa

It is crucial to broaden exploration beyond known taxa, as the majority of research conducted thus far has concentrated on cultivable bacteria and fungi, frequently from restricted geographic areas or plant tissues (Janarthine et al., 2011, Savitri et al., 2023). *A. marina* hosts a considerable and underexplored variety of endophytes, such as rare actinobacteria, non-culturable bacteria, and novel fungal lineages, which may possess unique genes and metabolic abilities. By employing systematic sampling across various environments, plant organs, and developmental stages, along with culture-independent methods, we can reveal this concealed diversity and its potential uses. Such endeavors will not only enhance our comprehension of mangrove microbiomes but also furnish new resources for biotechnology, agriculture, and environmental management

CONCLUSIONS

Avicennia marina is a habitat for a variety of endophytic microbes that serve essential ecological functions, such as improving the plant's ability to tolerate stress and disease and facilitating nutrient cycling in the challenging conditions of mangrove ecosystems. With their antioxidant, antimicrobial, anticancer, and enzymatic activities, these endophytes produce a diverse array of bioactive metabolites that are valuable for drug discovery and environmental remediation. Nevertheless, obstacles like cultivation difficulties, limited genomic data, and scalability issues prevent the complete utilization of their potential. Future investigations that combine omics technologies and synthetic biology with a more extensive examination of microbial diversity hold the potential to reveal novel applications in biotechnology, medicine, and ecosystem restoration, with *A. marina* endophytes emerging as crucial assets for sustainable innovation.

Supplementary materials
Not applicable.

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