Journal of Applied Botany and Green Economy
1(1): 2026

Review Article

Plant-Derived Terpenes: Biosynthesis, Classification and Applications

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Abstract

Terpenes represent one of the largest and most structurally diverse classes of plant secondary metabolites, playing essential roles in plant growth, development, and interactions with the biotic and abiotic environment. While extensive literature exists on terpene classification and biosynthesis, much of the current knowledge remains fragmented across biochemical, ecological, and applied research domains. Recent advances have highlighted terpenes not merely as end products of secondary metabolism but as multifunctional chemical mediators involved in plant defense, signaling, stress adaptation, and interactions with other organisms. This review critically synthesizes current understanding of plant-derived terpenes by integrating their biosynthetic origins with functional roles in ecological processes and emerging applications in agriculture, pharmaceuticals, food, and cosmetic industries. Rather than providing a purely descriptive account, in present study regulatory aspects of terpene biosynthesis, context-dependent biological functions, and key challenges that limit their translational exploitation were explored. Finally, we identify major knowledge gaps and future research directions, emphasizing the need for integrative and interdisciplinary approaches to fully harness the ecological and applied potential of plant terpenes.

Keywords: biosynthesis**,** classification, pharmaceutical, secondary metabolite, stress

Received: 24 November 2025 **Accepted**: 20 January 2026 **Published**: 31 January 2026

Citation: Malik A.,, A. Bibi, Tooba,J. Nasir, A. Akbar, M. Awais, K. Shahzadi, S. Fatima, A. Aslam, E. Fatima, I. Umbreen, N. Haneef, , M. Saeed, F. Sajid (2026). Plant-Derived Terpenes: Biosynthesis, Classification and Applications. Journal of Applied Botany and Green Economy. 1 (1): 102-138

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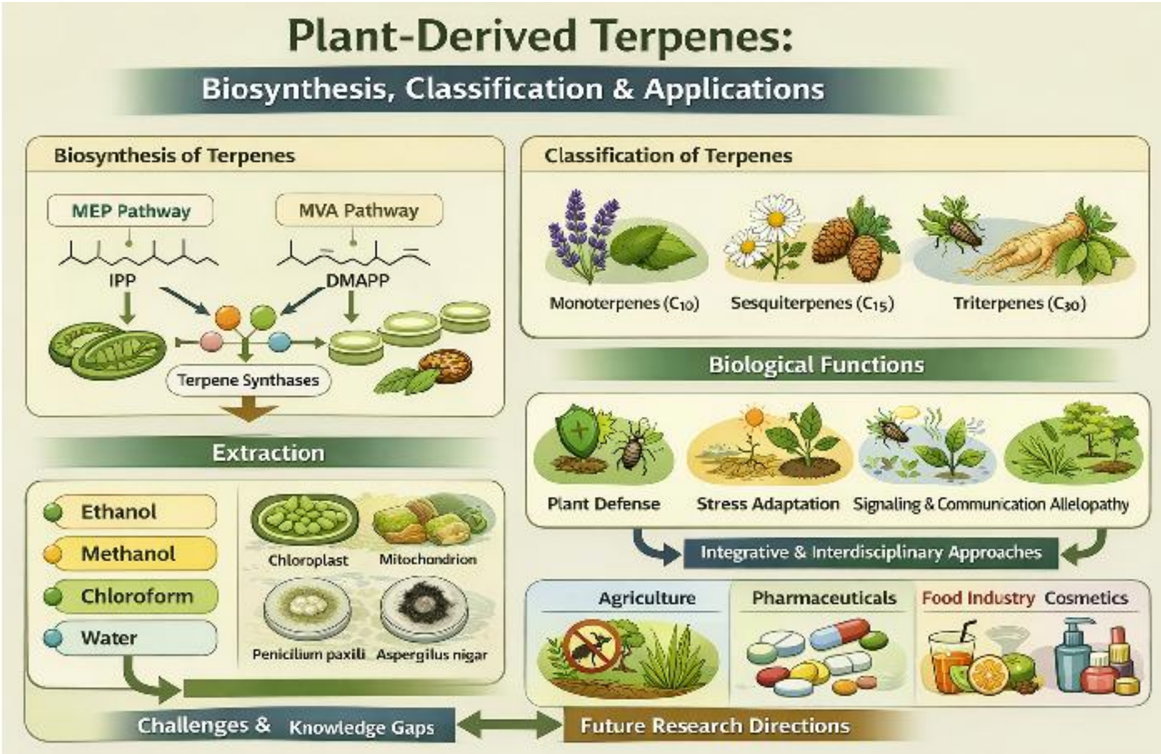
Graphical Abstract



1: Introduction

Plants synthesize a vast array of secondary metabolites that enable them to survive, adapt, and interact with their environment **(**Hazzoumi, 2019). Among these metabolites, terpenes constitute the largest and most chemically diverse group, encompassing more than 80,000 known compounds (Vranová *et al*., 2013; Gershenzon & Dudareva, 2007). These molecules are widely distributed across plant taxa and exhibit remarkable structural variation derived from the assembly and modification of isoprene units (Tholl, 2015)**.** Historically, terpenes were regarded as metabolic byproducts with limited biological relevance; however, this view has fundamentally shifted over the past few decades (Pichersky & Raguso, 2018)**.**

Accumulating evidence now demonstrates that terpenes are integral components of plant physiological processes, ecological interactions, and adaptive responses to environmental stresses (Gershenzon & Dudareva, 2007).Terpenes participate in a wide range of biological functions, including direct and indirect defense against herbivores and pathogens, attraction of pollinators and seed dispersers, allelopathic interactions with neighboring plants, and modulation of plant responses to abiotic stresses such as drought, salinity, and temperature extremes (Unsicker *et al*., 2009; Holopainen & Gershenzon, 2010). These functions are often context-dependent, varying with developmental stage, tissue type, and environmental conditions (Dudareva *et al*., 2013)**.** Such multifunctionality positions terpenes at the intersection of metabolism, ecology, and evolution, underscoring their importance beyond traditional chemical classification schemes (Pichersky & Raguso, 2018).

Although numerous reviews have addressed terpene biosynthesis, structural diversity, and specific applications, much of the existing literature remains compartmentalized (Vranová *et al*., 2013; Tholl, 2015). Biochemical studies frequently focus on pathway elucidation, ecological research emphasizes signaling and defense, and applied studies target pharmaceutical or industrial uses, often without integrating these perspectives (Dudareva *et al*., 2013).

As a result, a comprehensive understanding of how terpene biosynthesis, regulation, and ecological function collectively influence their applied potential is still lacking (Pichersky & Raguso, 2008). This fragmentation limits both theoretical progress and the effective translation of terpene research into sustainable agricultural and industrial practices (Gershenzon & Dudareva, 2007).

Recent advances in molecular biology, genomics, and chemical ecology have renewed interest in terpene research. Improved analytical tools and functional studies have revealed complex regulatory networks controlling terpene biosynthesis, including pathway crosstalk, spatial compartmentalization, and regulation by developmental and environmental cues (Vranová *et al*., 2013). At the same time, growing demand for natural products and environmentally friendly alternatives has intensified efforts to exploit plant terpenes for pharmaceutical, food, cosmetic, and agricultural applications (Langevald *et al.*, 2014). These developments highlight the need for an updated and integrative review that critically evaluates terpene research across disciplinary boundaries.

In this review, emphasis was on current knowledge on plant-derived terpenes by linking their classification and biosynthetic pathways with functional roles in plant defense, ecological interactions, and applied uses. The main object was to understanding terpenes as multifunctional metabolites rather than isolated chemical entities. Authors also discuss current limitations, unresolved questions, and future research priorities, with particular attention to strategies that may enhance the sustainable utilization of terpenes in agriculture and industry.

1.1: Classification of Terpenes:

Terpenes are traditionally classified according to the number of isoprene (C_5H_8) units that constitute their carbon skeleton, a framework commonly referred to as the isoprene rule (Vranová *et al*., 2013). Although this classification is chemically simple, it also provides important biological insight, as terpene size strongly influences volatility, subcellular localization, and functional roles in plants (Figure 1) (Gershenzon & Dudareva, 2007).

1.1.1: Hemiterpenes (C_5) represent the simplest terpene class and are primarily associated with volatile emissions involved in stress responses and atmospheric interactions. Monoterpenes (C_{10}) and sesquiterpenes (C_{15}) constitute the dominant fraction of plant volatile organic compounds and play central roles in plant–insect interactions, indirect defense signaling, and pollinator attraction (Dudareva *et al*., 2013; Tholl, 2015). Their relatively low molecular weight and high volatility enable rapid diffusion, making them effective mediators of short- and long-range ecological communication.

1.1.2: Diterpenes (C_{20}) are generally less volatile and are frequently associated with structural, defensive, and regulatory functions, including phytohormone biosynthesis (e.g., gibberellins) and antimicrobial defense compounds. Higher terpenes, including triterpenes (C_{30}) and tetraterpenes (C_{40}), are predominantly non-volatile and often function as membrane components, pigments, or signaling precursors, as exemplified by sterols and carotenoids (Tholl, 2015).

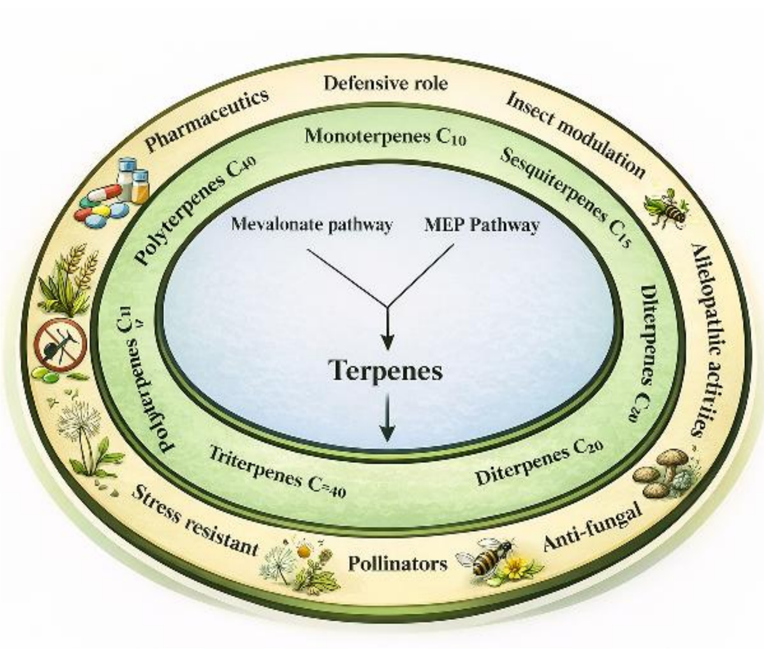


Figure 1: Integrated classification of plant terpenes highlighting carbon skeleton size, biosynthetic origin, volatility, representative compounds, and major biological functions. Terpene size is closely associated with subcellular biosynthetic compartmentalization and functional specialization, emphasizing the importance of interpreting terpene diversity in a biological and ecological context rather than purely chemical terms.

Beyond chemical classification, terpene classes are closely linked to biosynthetic compartmentalization, with monoterpenes and diterpenes largely synthesized via the plastidial MEP pathway, whereas sesquiterpenes and triterpenes are mainly produced through the cytosolic mevalonate pathway (Table 1). This spatial separation contributes to functional specialization and regulatory complexity, reinforcing the need to interpret terpene classification in a biological rather than purely chemical context (Vranová *et al*., 2013). Taken together, terpene classification provides a useful framework for understanding not only structural diversity but also functional differentiation, ecological relevance, and applied potential. However, future studies must move beyond static classification schemes to integrate regulatory control, environmental responsiveness, and metabolic plasticity, particularly in the context of sustainable exploitation and metabolic engineering (Table 1).

1.2: Biosynthetic pathway of terpenes

Terpene biosynthesis in plants is based on the universal five-carbon building blocks isopentenyl diphosphate (IPP) and dimethylallyl diphosphate (DMAPP). These precursors are synthesized through two spatially and biochemically distinct pathways: the cytosolic mevalonate (MVA) pathway and the plastidial methylerythritol phosphate (MEP) pathway. The compartmentalization of these pathways provides regulatory flexibility and contributes to the vast diversity of terpene structures observed in plants (Patil *et al.*, 2025).

Table 1: Classification of terpenes

Terpene Class	Carbon Units	Main Pathway	Volatility	Key Functions	Examples	Reference
Hemiterpenes	C5	MEP	High	Stress signaling	Isoprene	Dudareva *et al.*, 2013; Tholl, 2015.
Monoterpenes	C10	MEP	High	Defense, pollination	Limonene	ChMabou *et al.*, 2021.
Sesquiterpenes	C15	MVA	Moderate	Defense, allelopathy	Farnesene	Awouafack *et al.*, 2013
Diterpenes	C20	MEP	Low	Hormones, defense	Gibberellins	Keeling & Bohlmann, 2006.
Triterpenes	C30	MVA	Non-volatile	Membranes, signaling	Sterols	Awouafack *et al.*, 2013
Tetraterpenes	C40	MEP	Non-volatile	Pigmentation	Carotenoids	Awouafack *et al.*, 2013

1.2.1: Mevalonate (MVA) Pathway

The MVA pathway operates primarily in the cytosol and endoplasmic reticulum and is responsible for the biosynthesis of sesquiterpenes, triterpenes, and polyterpenes (Figure 2). This pathway begins with the condensation of acetyl-CoA units, leading to the formation of mevalonic acid, which is subsequently phosphorylated and decarboxylated to generate IPP. In cytosol IPP is then isomerized to DMAPP, allowing chain elongation reactions catalyzed by prenyltransferases (Bergmam *et al.*, 2019)

Figure 2: Mevalonate pathway showing sequential enzymatic steps leading to IPP and DMAPP formation, with key regulatory points highlighted

1.2.2: Methylerythritol Phosphate (MEP) Pathway

The MEP pathway is localized within plastids and supplies precursors for the biosynthesis of monoterpenes, diterpenes, tetraterpenes, and certain hemiterpenes. This pathway begins with the condensation of pyruvate and glyceraldehyde-3-phosphate, forming 1-deoxy-D-xylulose-5-phosphate, which is subsequently converted to IPP and DMAPP through a series of enzymatic reactions (Figure 3).The plastidial localization of the MEP pathway links terpene biosynthesis with photosynthetic activity, enabling rapid responses to light and stress conditions.

Crosstalk between the MEP and MVA pathways allows metabolic exchange of intermediates, further enhancing biosynthetic plasticity (Bergmam *et al*., 2019)

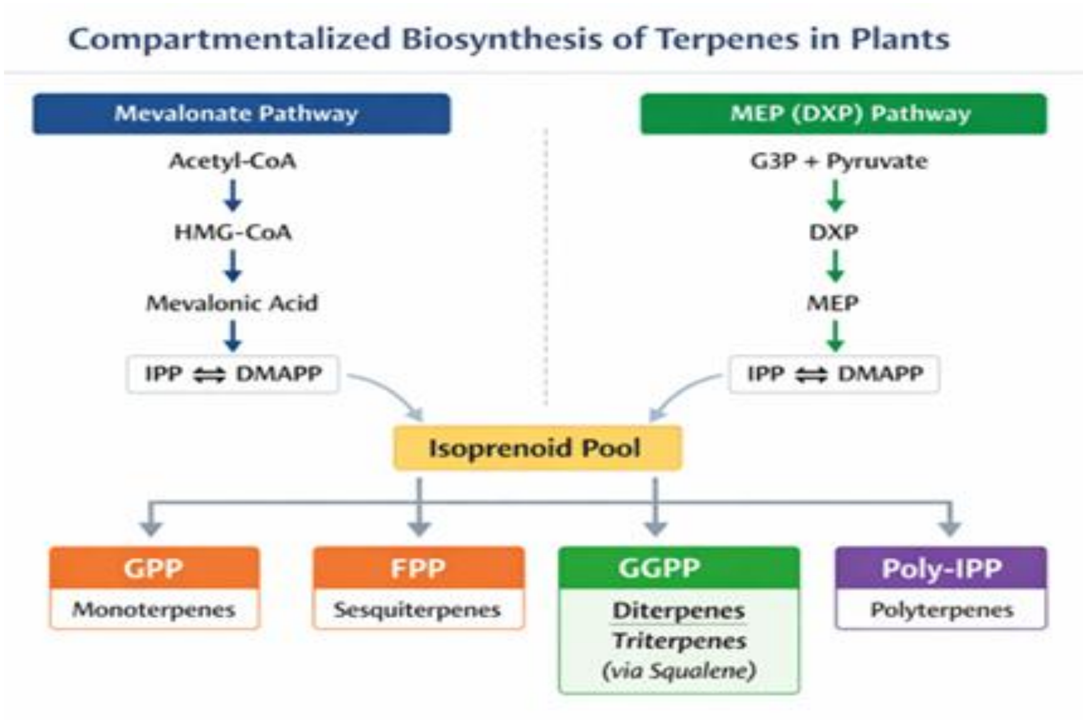


Figure 3. Compartmentalized biosynthesis of terpenes in plants.

Terpene biosynthesis originates from two distinct metabolic routes: the cytosolic mevalonate (MVA) pathway and the plastidial methylerythritol phosphate (MEP) pathway. Both pathways generate the universal C_5 isoprene units isopentenyl diphosphate (IPP) and dimethylallyl diphosphate (DMAPP), which form a central isoprenoid pool. Sequential condensation reactions yield geranyl diphosphate (GPP), farnesyl diphosphate (FPP), and geranylgeranyl diphosphate (GGPP), serving as direct precursors for mono-, sesqui-, di-, tri-, and polyterpenes. Crosstalk between the two pathways contributes to terpene diversity and metabolic flexibility in plants

1.2.3 Prenyltransferases and Terpene Synthases

Chain elongation reactions catalyzed by prenyltransferases produce geranyl diphosphate (GPP), farnesyl diphosphate (FPP), and geranylgeranyl diphosphate (GGPP), which serve as direct precursors for mono-, sesqui-, and diterpenes, respectively (Figure 4). Terpene synthases then catalyze cyclization and rearrangement reactions that generate the diverse terpene skeletons found in plants. Terpene synthases represent a large and functionally diverse enzyme family, and subtle changes in active-site architecture can result in dramatically different products. This enzymatic plasticity is a key driver of terpene chemical diversity.

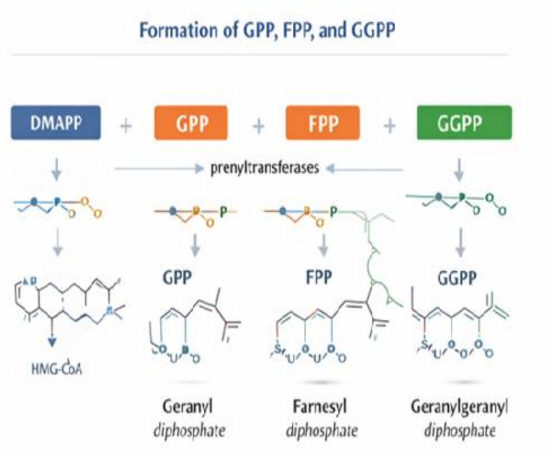


Figure 4: Biosynethesis of Geranyl diphosphate, Farnesyl diphosphate and Geranylgeranyl diphosphate

2: Regulation and Metabolic Integration

Terpene biosynthesis is tightly regulated at transcriptional, post-transcriptional, and post-translational levels. Transcription factors, substrate availability, and subcellular compartmentalization collectively determine terpene profiles in specific tissues and developmental stages. Additionally, environmental stresses such as herbivory, pathogen attack, drought, and temperature fluctuations strongly influence terpene biosynthetic activity. Understanding regulatory networks controlling terpene biosynthesis is essential for metabolic engineering strategies aimed at enhancing terpene production for pharmaceutical, agricultural, and industrial applications (Figure 5).

Terpene biosynthesis is regulated through coordinated interactions between the cytosolic mevalonate (MVA) pathway and the plastidial methylerythritol phosphate (MEP) pathway. Both pathways generate the universal isoprenoid precursor's isopentenyl diphosphate (IPP) and dimethylallyl diphosphate (DMAPP), which contribute to a shared isoprenoid pool. Transcription factors, terpene biosynthetic enzymes (including terpene synthases and key pathway enzymes), and metabolic crosstalk between cellular compartments collectively modulate flux toward different terpene classes. Environmental stimuli (light, temperature, herbivores, and pathogen attack) and phytohormones further fine-tune terpene production in a tissue- and development-dependent manner

3: Defensive Role of Terpenes in Plants

Terpenes constitute one of the most important classes of plant secondary metabolites involved in defense against both biotic and abiotic stresses. Their remarkable structural diversity, volatility, and chemical reactivity enable plants to deploy terpenes as direct toxins, repellents, signaling molecules, and indirect defense agents. Terpene-mediated defense operates at multiple biological levels, including deterrence of herbivores, inhibition of pathogens, and modulation of ecological interactions within plant communities (Gershenzon & Dudareva, 2007; Tholl, 2015)

.3.1: Antimicrobial and Antipathogenic Defense

Terpenes play a crucial role in plant defense against bacterial, fungal, and viral pathogens. Numerous monoterpenes and sesquiterpenes exhibit broad-spectrum antimicrobial activity by disrupting microbial cell membranes, increasing permeability, and interfering with essential metabolic enzymes (Bakkali *et al*., 2008). Oxygenated terpenoids, such as aldehydes and ketones, often display enhanced antimicrobial efficacy due to their higher reactivity. Diterpenes and triterpenes frequently function as phytoalexins low-molecular-weight antimicrobial compounds synthesized de novo in response to pathogen invasion (Figure 7). These compounds accumulate at infection sites and inhibit pathogen growth and spread (Ahuja *et al*., 2012). Importantly, mixtures of terpenes often show synergistic effects, providing more effective defense than individual compounds alone.

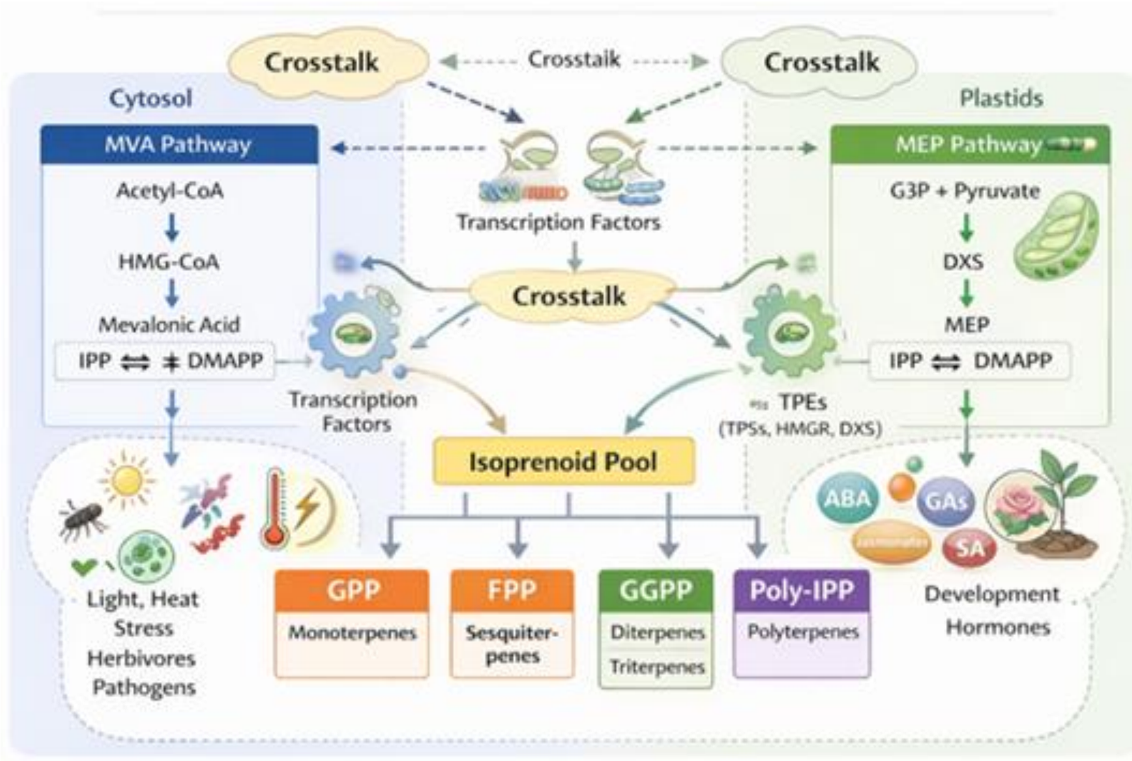


Figure 5. Integrated regulation of terpene biosynthesis in plants.

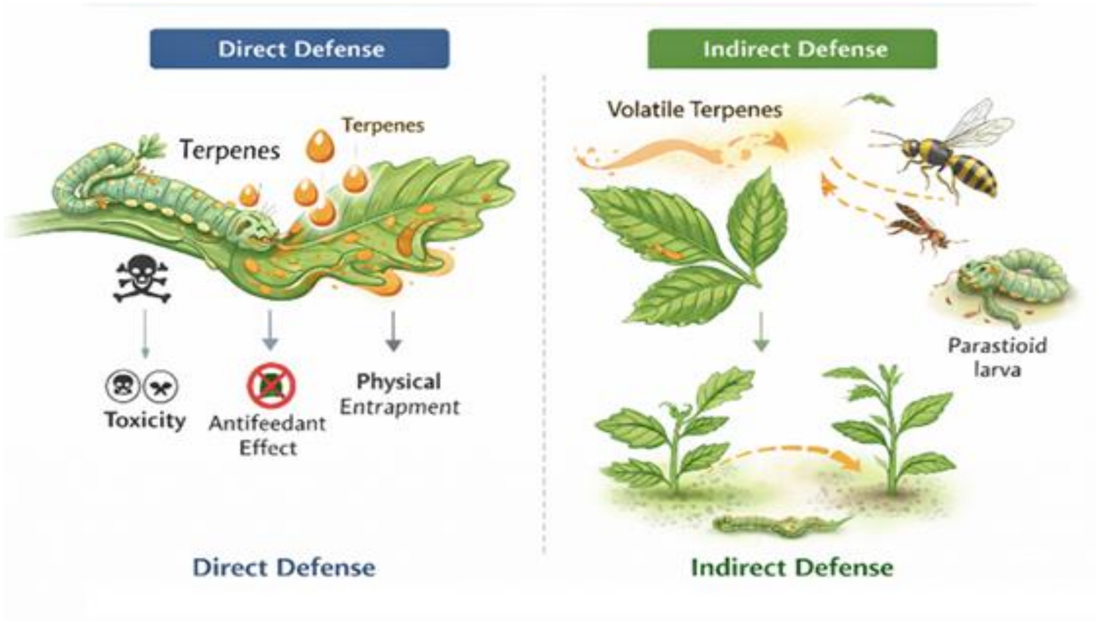


Figure 6: Terpene-mediated direct and indirect defense responses against herbivores

Table 2: Examples of direct defensive mechanism

Plant Species	Chemical	Terpene Type	Effect	Reference
Lavender *(Lavandula angustifolia)*	Linalool	Monoterpenoid	Repel Herbivores	(Ahuja *et al.*,2010)
Eucalyptus *(Eucalyptus globulus)*	1,8-Cineole	Monoterpene	Repels herbivores	(Oates *et al.*,2015)
Cannabis *(Cannabis sativa)*	β-Caryophyllene	Sesquiterpene	Protect from herbivores	(Gonçalves *et al.*,2020)
Neem *(Azadirachta indica)*	Azadirachtin	Triterpene	Inhibits insects growth	(Dave *et al.*, 2023)
Ginger *(Zingiber officinale)*	Zingiberene	Sesquiterpene	Exhibit antimicrobial	(Aleem *et al.*, 2020)
Tea tree *(Melaleuca alternifolia)*	Terpinen-4-ol	Monoterpene alcohol	Deters insects	(Carson *et al.*, 2006)

3.2: Indirect Defense and Ecological Signaling

Beyond direct toxicity, terpenes are central mediators of indirect plant defense through ecological signaling. Herbivore-induced volatile terpenes act as airborne cues that attract predators and parasitoids of herbivores, thereby reducing herbivore pressure (Table 3). This indirect defense strategy has been widely documented and represents a key component of plant insect enemy multitrophic interactions (Dicke & Baldwin, 2010). Terpenes also participate in plant–plant communication, where volatile emissions from damaged plants prime neighboring individuals for enhanced defensive responses (Figure 8). Such priming leads to faster and stronger activation of defense pathways upon subsequent attack, highlighting the role of **t**erpenes in community-level defense dynamics (Heil & Karban, 2010).

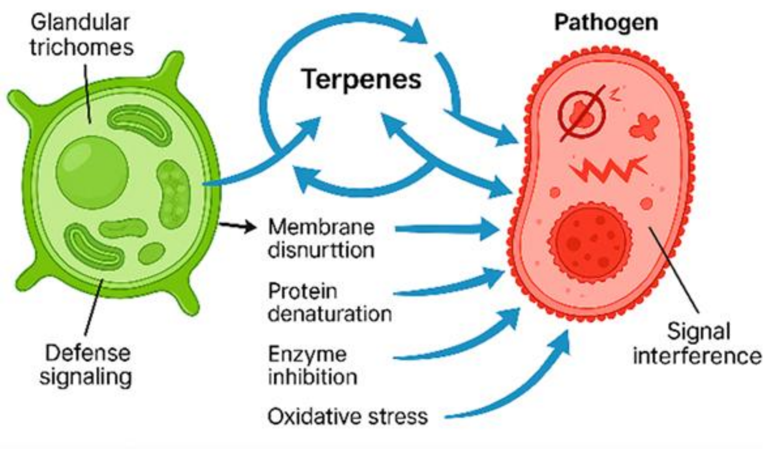


Figure 7: Antimicrobial mechanisms of terpene action in plant defense

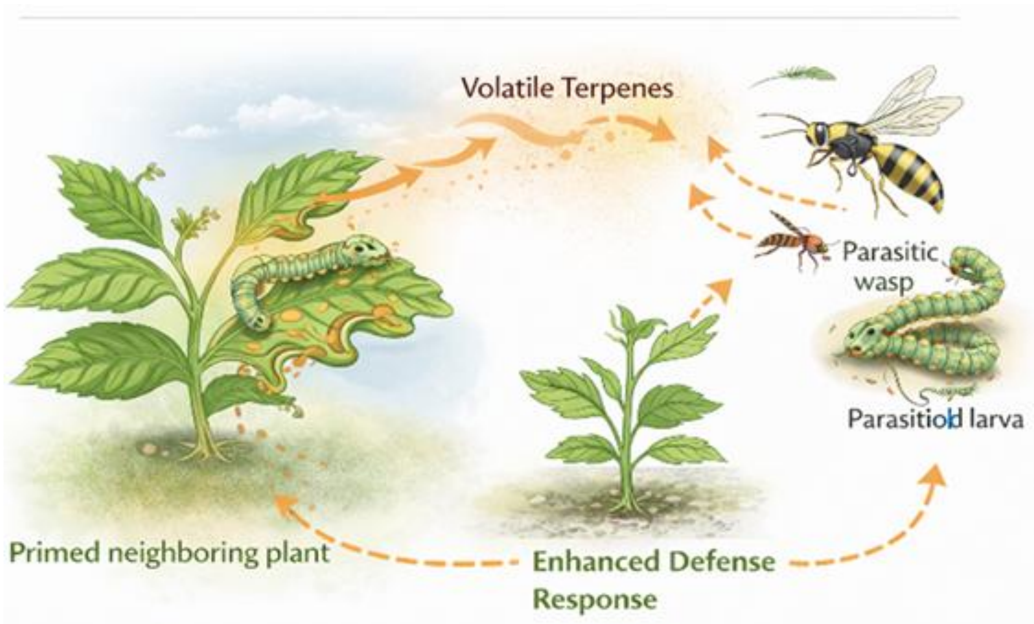


Figure 8: Volatile terpene signaling in plant–insect–enemy interactions

3.3: Protection against Abiotic Stress

In addition to biotic defense, certain terpenes contribute significantly to plant tolerance against abiotic stresses (Figure 9). Hemiterpenes, particularly isoprene, protect photosynthetic membranes against thermal and oxidative stress by stabilizing lipid bilayers and scavenging reactive oxygen species (Vickers *et al*., 2009). Carotenoids, a major class of tetraterpenes, play essential photoprotective roles by dissipating excess excitation energy and quenching singlet oxygen, thereby preventing photooxidative damage under high light and stress conditions (Table 4) (Niyogi *et al*., 2005).

Table 3: Indirect Defensive Mechanism of Terpenes in Different Angiospermic Plant Species

Plant	Type of Terpene	Role	Reference
Tomato *(Lycopersicon escustentum)*	monoterpenes and sesquiterpenes	Poisonous for pests.	(Block *et al.*,2019)
Maize (*Zea Mays)*	Sesquiterpenes	Attract stinging parasites that destroyed the caterpillars which is susceptible for disease.	(Block *et al.*,2019)
Lima bean (*Phaseolus lunatus*)	Homoterpenes, (DMNT, TMTT)	Attract predators of herbivores like predatory mites.	(Sharma *et al.*,2017)
Cotton (*Gossypium hirsutism*)	Terpenoids (Gossypol)	Attract parasitoid wasps to larvae feeding on cotton	(LyOpitz *et al.*,2008)
Apple (*Pyrus malus*)	Sesquiterpenes (β-farnesene)	Attract natural enemies of aphids feeding on apple leaves	(Badra *et al.*,2021)
Pine *(Pinus spp)*	Monoterpenes (limonene)	Attract the predators of bark beetles	(Groenewold *et al.*,2025).

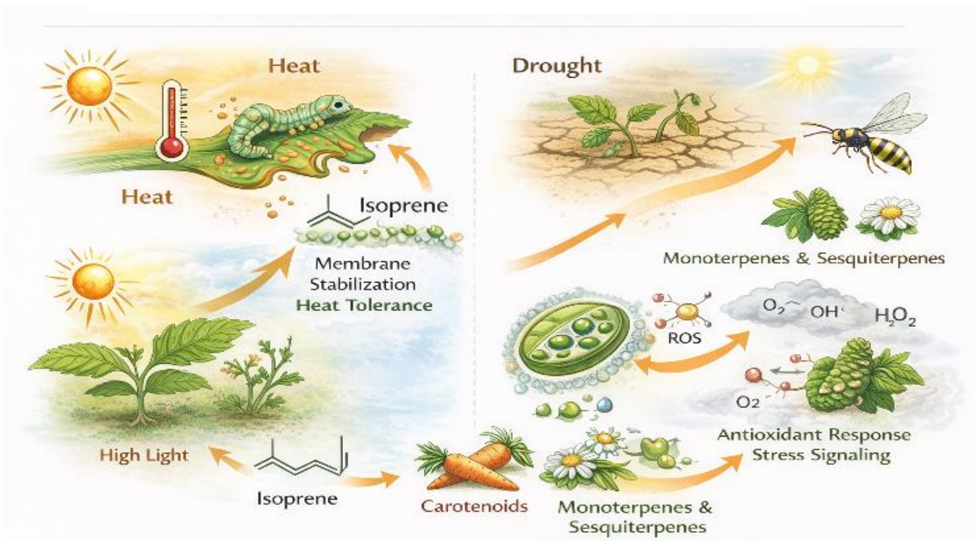


Figure 9: Protective roles of terpenes under abiotic stress conditions

3.4: Integration with Biosynthetic Regulation

The defensive roles of terpenes are tightly linked to their biosynthetic regulation. Environmental stimuli such as herbivory, pathogen attack, drought, and temperature stress activate signaling pathways involving jasmonic acid, salicylic acid, and ethylene, which in turn regulate terpene biosynthetic genes and terpene synthase activity (Wasternack & Hause, 2013; Tholl, 2015). Crosstalk between the cytosolic MVA and plastidial MEP pathways allows flexible redistribution of metabolic flux toward defense-related terpene production, reinforcing the adaptive significance of terpene diversity in plants (Figure 10).

4: Terpenes in Modulating Insect Behaviour

Terpenes are among the most influential plant secondary metabolites governing plant–insect interactions. Through their function as volatile and non-volatile semiochemicals, terpenes regulate insect orientation, feeding behavior, oviposition, mating, and multitrophic interactions. Their behavioral effects are mediated through insect chemosensory and neurophysiological

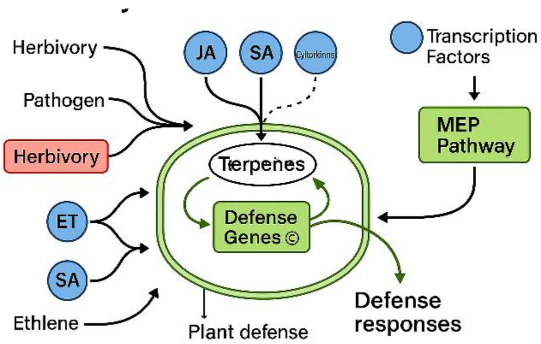


Figure 10: Integrated regulation of terpene biosynthesis in plant defense

systems and are tightly linked to terpene biosynthetic regulation and ecological context (Gershenzon & Dudareva, 2007; Tholl, 2015).

4.1: Terpenes as Olfactory Signals in Host Location

Volatile terpenes emitted from vegetative and reproductive tissues play a central role in insect host-location processes. Monoterpenes and sesquiterpenes such as linalool, α-pinene, β-myrcene, and limonene are detected by insect olfactory receptor neurons and guide long-range orientation toward host plants (Degenhardt *et al*., 2009). Insects often rely on complex terpene blends rather than single compounds, using both qualitative composition and quantitative ratios to discriminate suitable hosts (Clavijo McCormick *et al*., 2012). Importantly, terpene-mediated attraction is highly context-dependent. Variations in terpene stereochemistry, emission dynamics, and plant physiological status can alter insect behavioral responses from attraction to avoidance (Holopainen & Gershenzon, 2010; Dudareva *et al*., 2013). Such plasticity allows plants to manipulate insect host-finding efficiency under changing environmental and ecological conditions (Figure 11). 4.2: Repellent and Deterrent Effects of Terpenes

Many terpenes act as repellents or antifeedants by over stimulating insect sensory systems or interfering with normal physiological processes. Monoterpenes including camphor, thymol, menthol, and 1, 8-cineole disrupt insect neurotransmission and sensory perception, leading to avoidance behavior and reduced feeding (Isman, 2006; Regnault-Roger *et al*., 2012). These effects are particularly pronounced in generalist herbivores

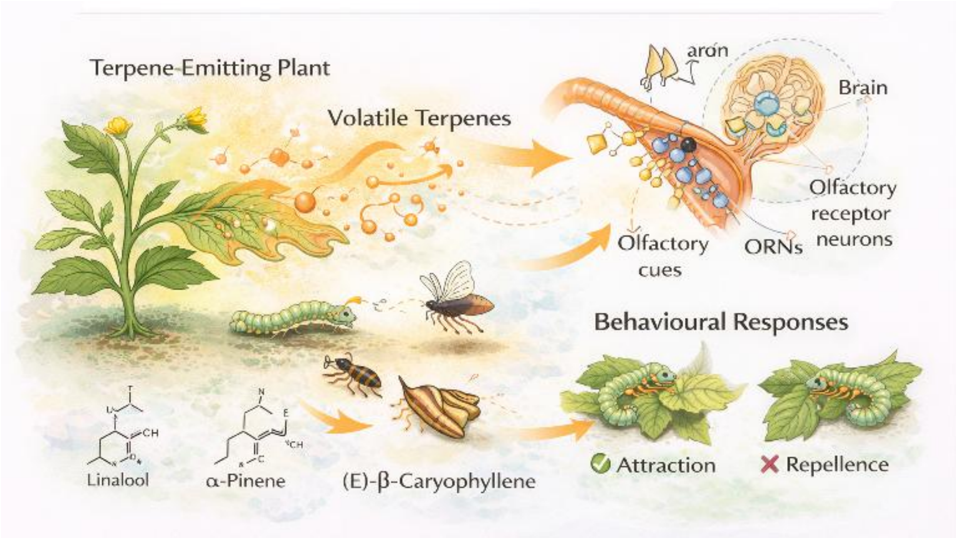


Figure 11: Terpene-mediated olfactory signaling in plant–insect interactions

Table 4: Plant Terpenes and their Role for biotic and abiotic stress management

Plant type	**Terpenes**	**Attack**	**Effects**	**Reference**
Dalechampia (Clusia spp.)	Oxygenated triterpenes	Apidae, Megachilidae, or worker Apidae	Pollinators for use in nest construction	*(Srivastava et al., 2024).*
Fig (*Ficus hispida*)	Monoterpenes: linalool, limonene and pinene	Wasp	Signals for pollinators	*(Srivastava et al., 2024)*
Maize (*Zea mays*)	terpene	*Cotesia marginventris* specialized parasitoid (Microplitis croceipes).	Attract oparasitoid	*Mitra et al.,2017)*
Tomato (*Lycopersicon esculentum*	b-ocimene	Parasitoid (Aphidius ervi	Attract parasitoids	*(Srivastava et al., 2024)*
Cucumber	Cucurbitacins	Spider mite (Tetranychusurticae)	antibiotic for spider mites	*(Mitra et al.,2017)*
Cabbage plants	monoterpene: 1,8-cineole	Parasitic wasps (Cotesia glomerata)	Attracts parasitoids that lay eggs	Ahuja *et al.,2010)*
Pineapple zamia	B-myrcene, (E)-_ ocimene	Thrips (*Cycadothrips chadwick*)	Attract pollinators	*(*Terry *et al.,2007)*

Lacking specialized detoxification mechanisms. Sesquiterpenes and sesquiterpene lactones often exhibit stronger deterrent activity due to their increased molecular complexity and reactivity. These compounds can inhibit digestive enzymes, disrupt ion channel function, and induce oxidative stress, resulting in reduced larval growth and survival (Chadwick *et al*., 2013; Unsicker *et al*., 2009). Notably, terpene mixtures frequently show synergistic effects, enhancing deterrence compared to individual constituents (Berenbaum & Zangerl, 2008).

4.2: Terpenes and Oviposition Behaviour

Terpenes strongly influence insect oviposition decisions by serving as chemical indicators of host suitability and defensive status. Elevated emission of specific monoterpenes and sesquiterpenes following herbivore damage often deters further egg-laying by conspecific females, thereby limiting subsequent infestation (*Srivastava et al.,* 2024). Such deterrent effects reduce offspring competition and exposure to toxic metabolites.Conversely, some specialist insects exploit terpene cues to identify preferred hosts with predictable chemical profiles. In these systems, terpenes act as reliable signals rather than deterrents, reflecting co-evolutionary adaptation between plants and herbivores (Bruce & Pickett, 2011).

4.3: Terpenes in Indirect Defense: Recruitment of Natural Enemies

One of the most ecologically significant roles of terpenes is their involvement in indirect plant defense via tritrophic interactions. Herbivore-induced plant volatiles (HIPVs), dominated by mono- and sesquiterpenes, attract predators and parasitoids of herbivorous insects, thereby reducing herbivore pressure (Dicke & Baldwin, 2010). Compounds such as (E)-β-caryophyllene, linalool, and ocimene are well-known attractants for natural enemies. Natural enemies typically respond to specific terpene blends rather than individual compounds, highlighting the importance of terpene diversity and emission dynamics (Dicke & Baldwin, 2010). This indirect defense mechanism significantly enhances plant fitness and represents a sophisticated form of chemical communication (Figure 12).

4.4: Neurophysiological Effects of Terpenes on Insects

At the molecular level, terpenes exert profound effects on insect nervous systems. Many monoterpenes interact with octopamine receptors, GABA-gated chloride channels, and acetylcholinesterase, leading to altered locomotion, feeding, and orientation behavior. These neurotoxic effects underpin the widespread use of terpene-rich essential oils as botanical insecticides. Species-specific differences in receptor sensitivity and detoxification capacity explain why certain terpenes selectively deter herbivores while having minimal effects on pollinators and natural enemies (Isman, 2020; Pavela & Benelli, 2016). This selectivity enhances the ecological value of terpenes as targeted defensive compounds

4.5: Evolutionary and Ecological Implications

The behavioral effects of terpenes reflect a long-standing co-evolutionary arms race between plants and insects (Table 3). Continuous herbivore pressure has driven diversification of terpene biosynthetic pathways, while insects have evolved sophisticated sensory and metabolic adaptations to cope with terpene exposure (Zangerl *et al.*, 2008). This reciprocal evolution contributes to the extraordinary structural and functional diversity of terpenes observed across plant taxa (Table 4).

5: Allelopathic Activities of Terpenes

Allelopathy refers to the chemical interactions among plants mediated by secondary metabolites that influence the growth, survival, and reproduction of neighboring organisms. Among these metabolites, terpenes play a prominent role as allelochemicals due to their abundance, volatility, persistence in soil, and broad biological activity. Terpene-mediated allelopathy contributes to plant competition, community structure, and ecosystem functioning, particularly in natural and agricultural systems (Inderjit *et al.*, 2011; Cheng & Cheng, 2015).

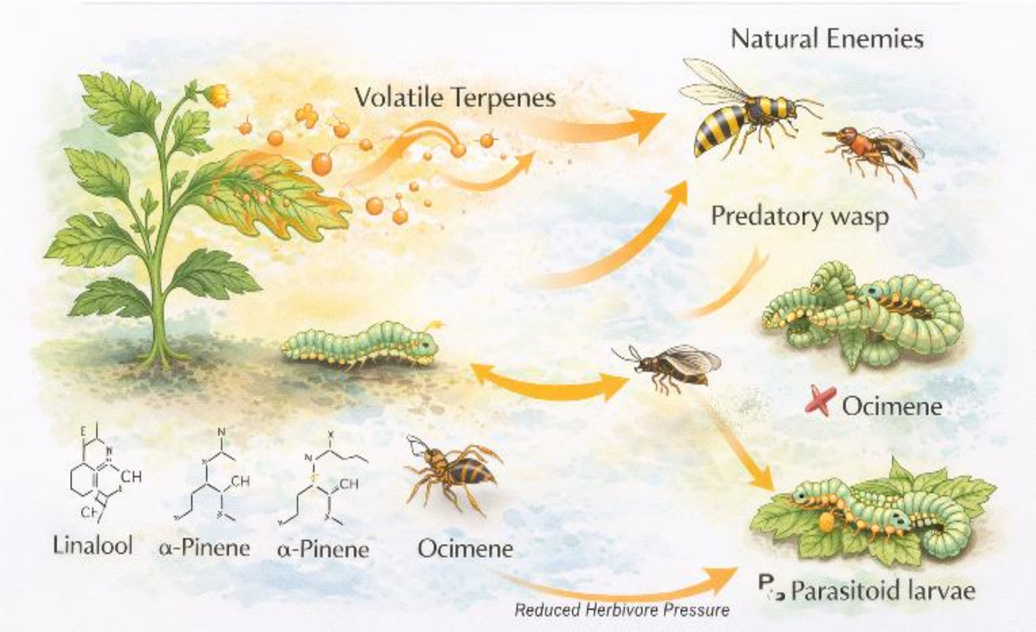


Figure 12: Volatile terpene-mediated tritrophic signaling among plants, herbivores, and natural enemies

Table 5. Influence of major terpene classes on insect behavior

Terpene class	Representative compounds	Behavioral effect	Ecological function	Key references
Monoterpenes	Limonene, linalool, α-pinene	Attraction/repellence	Host location	Dudareva *et al*., 2013
Sesquiterpenes	(E)-β-caryophyllene	Predator attraction	Indirect defense	Dicke & Baldwin, 2010
Diterpenes	Resin acids	Feeding inhibition	Direct defense	Keeling & Bohlmann, 2006
Triterpenes	Saponins	Growth suppression	Anti-feedant	Osbourn *et al*., 2011

5.1: Sources and Release Pathways of Allelopathic Terpenes

Allelopathic terpenes are released into the environment through multiple pathways, including volatilization from aerial tissues, leaching from leaves, root exudation, and decomposition of plant residues (Figure 13). Monoterpenes and sesquiterpenes are especially effective allelochemicals due to their high volatility and lipophilicity, allowing them to diffuse through air and soil matrices (Inderjit *et al*., 2011). Aromatic plants such as *Salvia*, *Eucalyptus*, *Artemisia*, and *Pinus* species are well-known producers of terpene-rich allelochemicals. In forest ecosystems, terpene emissions from litter and roots can create chemically inhospitable zones that suppress understory vegetation, thereby reducing competition for resources (Cheng & Cheng, 2015; Kato-Noguchi, 2017)

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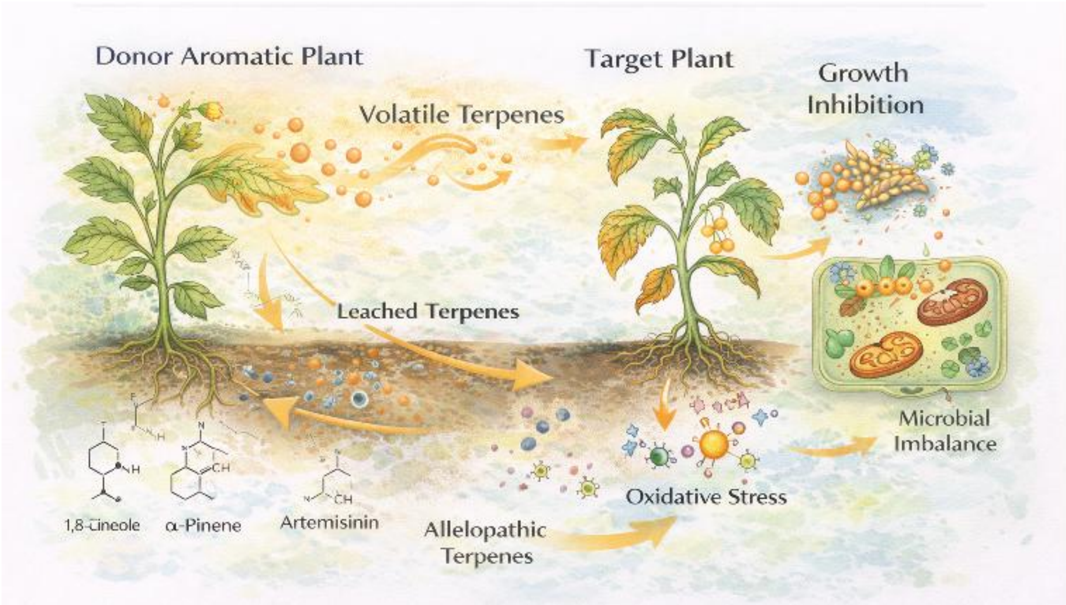

Figure 13: Release pathways and environmental fate of allelopathic terpenes

5.2: Effects of Terpenes on Seed Germination and Seedling Growth

Terpenes exert strong inhibitory effects on seed germination and early seedling development, which are critical stages in plant establishment. Monoterpenes such as 1,8-cineole, camphor, α-pinene, and limonene have been shown to delay germination, reduce radicle elongation, and suppress hypocotyl growth in a wide range of plant species. These effects are concentration-dependent and often species-specific, suggesting selective allelopathic interactions. Sesquiterpenes and diterpenes may exert more persistent inhibitory effects due to lower volatility and higher soil retention, contributing to long-term suppression of competing vegetation (Kato-Noguchi *et al.*, 2017; Macías *et al*., 2007).

5.3: Physiological and Cellular Mechanisms of Allelopathic Action

At the physiological level, allelopathic terpenes interfere with fundamental cellular processes in target plants. Reported mechanisms include disruption of cell membrane integrity, inhibition of mitochondrial respiration, alteration of ion transport, and suppression of photosynthetic activity. Lipophilic terpenes readily penetrate lipid bilayers, leading to increased membrane permeability and leakage of cellular contents. Additionally, terpenes induce oxidative stress by promoting the accumulation of reactive oxygen species (ROS), resulting in lipid peroxidation, protein oxidation, and DNA damage (Figure 14). These effects collectively impair cellular metabolism and growth, ultimately leading to growth inhibition or plant death (Cheng & Cheng, 2015).

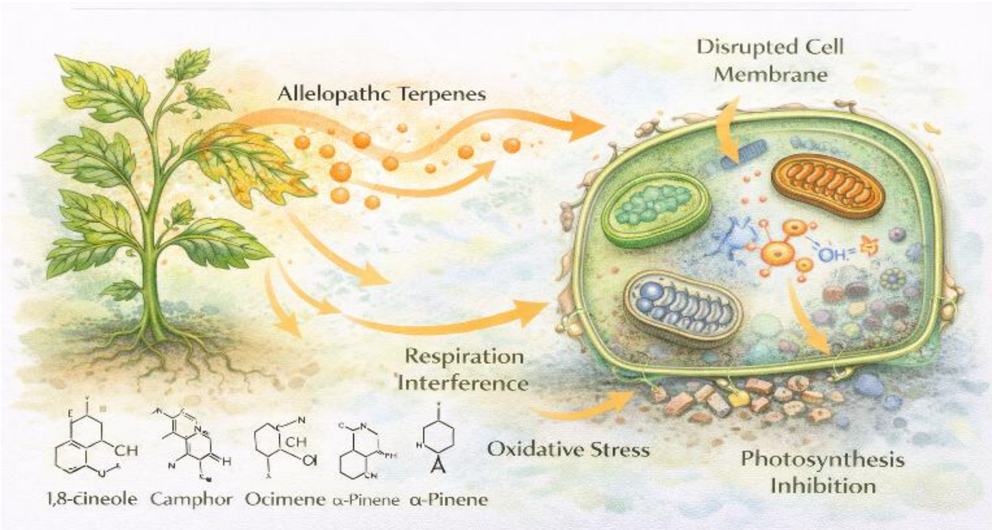

Figure 14: Cellular and physiological targets of allelopathic terpenes in plants

5.4: Influence on Soil Microbial Communities

Beyond direct phytotoxicity, terpenes indirectly affect plant growth by modulating soil microbial communities. Many terpenes exhibit antimicrobial activity, altering microbial composition and enzymatic activity in the rhizosphere. Such changes can influence nutrient cycling, organic matter decomposition, and symbiotic interactions, further shaping plant competitive outcomes. In some cases, terpene-mediated suppression of beneficial microbes reduces nutrient availability to neighboring plants, amplifying allelopathic effects. Conversely, selective stimulation of specific microbial taxa may enhance degradation of allelochemicals, highlighting the dynamic nature of terpene–microbe interactions (Inderjit *et al*., 2011).

5.5: Ecological and Evolutionary Significance of Terpene Allelopathy

Terpene-mediated allelopathy has profound ecological implications, influencing plant distribution, species dominance, and successional patterns (Table 7). Invasive plant species often exploit allelopathic terpenes to outcompete native flora, a phenomenon described as the "novel weapons hypothesis" (Inderjit *et al.*, 2011). From an evolutionary perspective, selection pressures imposed by plant–plant competition have driven diversification of terpene biosynthetic pathways, resulting in structurally diverse allelochemicals with distinct modes of action. This chemical diversity enhances competitive fitness and contributes to ecosystem-level chemical heterogeneity (Macías *et al.*, 2007).

Table 7. Allelopathic effects of major terpene classes on plant growth

Terpene class	Representative compounds	Target effect	Mode of action	Key references
Monoterpenes	1,8-Cineole, α-pinene	Germination inhibition	Membrane disruption, ROS	Kato-Noguchi *et al.*, 2017
Sesquiterpenes	Artemisinin	Seedling growth suppression	Metabolic inhibition	Macías *et al.*, 2007
Diterpenes	Cafestol	Root growth inhibition	Respiration interference	Kato-Noguchi, 2017
Triterpenes	Saponins	Nutrient uptake reduction	Membrane permeabilization	Osbourn *et al.*, 2011

6: Anti-Fungal and Anti-Microbial Activities of Terpenes

Terpenes constitute one of the most potent and diverse groups of plant-derived antimicrobial agents. Owing to their structural diversity, lipophilicity, and reactivity, terpenes exhibit broad-spectrum activity against bacteria, fungi, and other pathogenic microorganisms. Their antimicrobial roles are ecologically significant for plant defense and have attracted increasing interest for pharmaceutical, agricultural, and food-preservation applications (Bakkali *et al.*, 2008; Tholl, 2015).

6.1: Antifungal Activity of Terpenes

Fungal pathogens pose a major threat to plant survival and agricultural productivity, and terpenes play a central role in antifungal defense. Monoterpenes such as thymol, carvacrol, 1,8-cineole, and α-pinene have demonstrated strong inhibitory effects against phytopathogenic fungi including *Fusarium*, *Alternaria*, *Botrytis*, and *Aspergillus* species (Pinto *et al.*, 2009; Nazzaro *et al.*, 2013). Sesquiterpenes and diterpenes often exhibit enhanced antifungal potency due to their lower volatility and higher persistence in tissues and soils. Sesquiterpene lactones disrupt fungal growth by interfering with membrane integrity and enzymatic activity, while diterpenes such as resin acids accumulate at infection sites as part of inducible defense responses (Keeling & Bohlmann, 2006; Chadwick *et al.*, 2013).

6.2: Antibacterial Activity of Terpenes

Terpenes exhibit antibacterial activity against both Gram-positive and Gram-negative bacteria, though Gram-positive bacteria are generally more susceptible due to the absence of an outer membrane. Monoterpenes such as limonene, linalool, and terpinen-4-ol disrupt bacterial cell membranes, leading to leakage of ions and metabolites. Gram-negative bacteria exhibit higher resistance due to lipopolysaccharide barriers; however, certain oxygenated terpenes and terpene mixtures can overcome this resistance through synergistic effects. Sesquiterpenes and triterpenes further inhibit bacterial growth by targeting intracellular enzymes, DNA synthesis, and energy metabolism (Nazzaro *et al*., 2013).

6.3: Mechanisms of Antimicrobial Action

6.3.1: Membrane Disruption and Permeabilization

The primary antimicrobial mechanism of terpenes involves disruption of microbial cell membranes. Due to their hydrophobic nature, terpenes partition into lipid bilayers, altering membrane fluidity and permeability. This leads to loss of membrane potential, leakage of cytoplasmic contents, and eventual cell lysis. Fungal membranes rich in ergosterol and bacterial membranes composed of phospholipids are particularly susceptible to terpene-induced destabilization, explaining the broad-spectrum antimicrobial activity of these compounds.

6.3.2: Induction of Oxidative Stress

Many terpenes induce oxidative stress in microbial cells by promoting excessive production of reactive oxygen species (ROS). Elevated ROS levels damage proteins, lipids, and nucleic acids, impairing cellular metabolism and viability (Gill & Holley, 2006; Tian *et al*., 2012). This oxidative damage often acts synergistically with membrane disruption to enhance antimicrobial efficacy.

6.3.4: Enzyme and Metabolic Inhibition

Terpenes can directly inhibit microbial enzymes involved in respiration, cell wall synthesis, and energy metabolism. In fungi, terpenes interfere with mitochondrial function and ATP synthesis, while in bacteria they inhibit enzymes involved in fatty acid and protein biosynthesis (Cristani *et al*., 2007; Di Pasqua *et al*., 2007).

6.4: Synergistic Effects and Complex Mixtures

One of the most significant features of terpene antimicrobial activity is the strong synergism observed in complex terpene mixtures, such as essential oils. Individual terpenes may show moderate activity, but when combined they often exhibit enhanced antimicrobial effects due to multi-target interactions (Bassolé & Juliani, 2012; Nazzaro *et al*., 2013). This synergism reduces the likelihood of resistance development and explains why whole essential oils are often more effective than isolated components. Synergistic interactions also occur between terpenes and conventional antimicrobial agents, enhancing antibiotic efficacy (Langeveld *et al*., 2014).

6.5: Role of Terpenes in Plant Defense Against Pathogens

In plants, antimicrobial terpenes function as both constitutive and inducible defenses (Table 8). Many plants store terpenes in specialized structures such as glandular trichomes and resin ducts, releasing them upon pathogen attack. Others synthesize terpenoid phytoalexins de novo in response to infection (Ahuja *et al*., 2012; Tholl, 2015). Activation of terpene biosynthesis during pathogen invasion is regulated by signaling pathways involving salicylic acid and jasmonic acid, linking antimicrobial terpene production to broader immune responses (Wasternack & Hause, 2013).

6.6: Agricultural and Medical Relevance

The antimicrobial properties of terpenes have significant implications for sustainable agriculture and medicine. Terpene-based formulations are increasingly explored as natural fungicides and bactericides due to their biodegradability and low environmental persistence (Isman, 2006; Pavela & Benelli, 2016). In medical contexts, terpenes exhibit activity against antibiotic-resistant pathogens and are being investigated as alternative or complementary antimicrobial agents. Their ability to disrupt membranes and act on multiple targets reduces the risk of resistance development (Langeveld *et al*., 2014).

7: Action against Molds

Terpenes exhibit strong antifungal activity against filamentous fungi (molds), which are responsible for severe plant diseases, postharvest losses, and mycotoxin contamination (Figure 15). Essential oils rich in terpene constituents such as eugenol, nerol, thymol, and carvacrol have demonstrated pronounced inhibitory effects against toxigenic and phytopathogenic molds, particularly species of *Aspergillus*, *Fusarium*, *Rhizoctonia*, and *Trichophyton* (Mihai & Popa, 2015; Pinto *et al*., 2009; Nazzaro *et al*., 2017).

Essential oils derived from citrus peels, dominated by d-limonene**,** exhibit potent antifungal activity against *Fusarium oxysporum* and *Rhizoctonia solani*, disrupting mycelial growth and inhibiting spore germination (Hu *et al*., 2023; Tian *et al*., 2012). Synergistic interactions among terpene mixtures further enhance antifungal efficacy. For instance, combinations of linalool and γ-terpinene effectively inactivate dermatophytic fungi such as *Trichophyton rubrum*, indicating multi-target modes of action (Thawabteh *et al*., 2023; Bassolé & Juliani, 2012)

9: Terpenes as Pollinator Attractants and Seed Disseminators

Terpenes play a crucial role in mediating mutualistic plant–pollinator interactions by acting as chemical cues and rewards. Certain pollinators have evolved remarkable tolerance or specialization toward terpene compounds that are otherwise toxic to insects.

Table 8. Antifungal and antibacterial activities of major terpene classes

Terpene class	Representative compounds	Target organisms	Primary mechanism	Key references
Monoterpenes	Thymol, carvacrol	Bacteria, fungi	Membrane disruption	Bassolé & Juliani, 2012
Sesquiterpenes	Farnesol	Fungi	Respiration inhibition	Pinto *et al*., 2009
Diterpenes	Resin acids	Phytopathogenic fungi	Cell wall damage	Keeling & Bohlmann, 2006
Triterpenes	Saponins	Fungi, bacteria	Membrane permeabilization	Osbourn *et al*., 2011

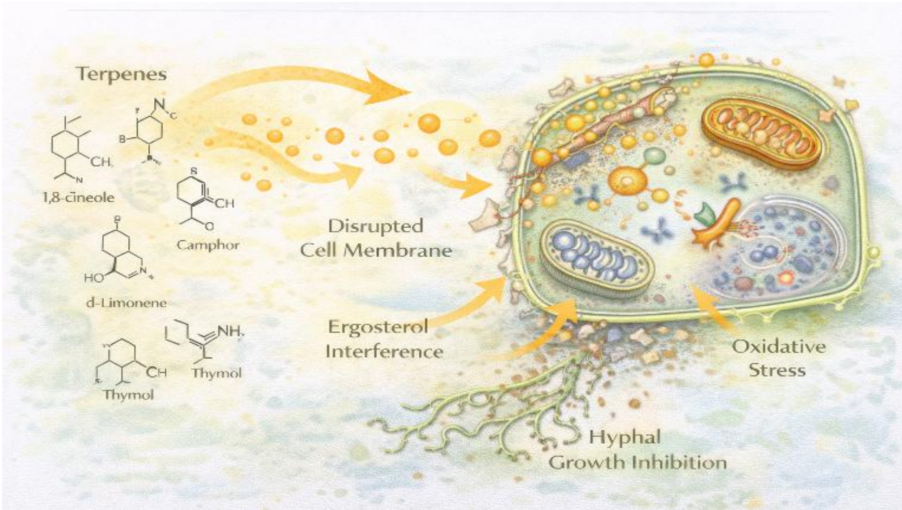

Figure 15: illustrates the principal cellular targets of terpene action in mold cells, including membrane destabilization, ergosterol interference, and oxidative stress induction.

Orchid bees (Euglossinae) collect monoterpenes such as 1,8-cineole from orchid and *Dalechampia* flowers, storing them in specialized leg structures and later releasing them during courtship displays to attract females (Boncan *et al.,* 2020; Tholl, 2015). In addition to pollination, triterpene-rich resins are collected by female bees (*Euglossini*, *Hypanthidium*, *Trigona*) for nest construction, simultaneously facilitating pollination (Boncan *et al*., 2020). Some flowering plants also serve as breeding sites for their pollinators, using terpenes as host-recognition signals. For example, noctuid moths (*Hadena bicruris*) locate *Silene latifolia* flowers by detecting lilac aldehydes emitted by the plant (Boncan *et al*., 2020).

10: Terpenes in Scent-Mediated Interactions

Volatile terpenoids released by flowers and fruits strongly influence interactions with pollinators and frugivores. Floral scent profiles dominated by terpenes convey information regarding nectar availability and pollen rewards. Linalool, a ubiquitous monoterpene alcohol, is a major attractant for bees, moths, and butterflies (Gao *et al*., 2018). Fruit-derived terpene blends enhance detectability and attractiveness to seed dispersers such as birds, bats, and mammals (Figure 16). Variation in terpene composition can significantly alter disperser preference, thereby influencing seed dispersal efficiency and spatial distribution (Nelson & Whitehead, 2021).

Figure 16: Depicts terpene-mediated olfactory signaling in plant–animal interactions

11: Applications in Pollination Biology

Understanding terpene-mediated attraction has practical implications in agriculture and conservation. Identification of crop-specific terpene attractants offers opportunities to enhance pollination efficiency and improve yield stability (He *et al*., 2022). In conservation biology, synthetic terpene blends are increasingly explored to support reproduction in rare or endangered plant species by selectively attracting native pollinators (Chen and Song, 2022).

Table 9: Summarizes representative terpenes, their microbial targets, and primary mechanisms of action

Terpene	Chemical Structure (Functional Group)	Microbial Targets	Primary Mechanism of Action	Key References
Thymol	Phenolic monoterpene (–OH group)	• Bacteria • Fungi	Membrane disruption leading to leakage of cellular contents	Cristani *et al*., 2007
Carvacrol	Phenolic monoterpene (–OH group)	• Fungi • *Mycobacterium tuberculosis*	Collapse of proton motive force and membrane depolarization	Andrade-Ochoa *et al*., 2015; Nazzaro *et al*., 2013
Farnesol	Sesquiterpene alcohol	• Fungi	Mitochondrial dysfunction and inhibition of energy metabolism	Pinto *et al*., 2009; Braga & Ricci, 2011
Linalool	Monoterpene alcohol	• Gram-positive bacteria • Gram-negative bacteria	Enzyme inhibition and disruption of metabolic pathways	Usach *et al*., 2020

11.1: Insect-Mediated Seed Dispersal

Insects also contribute to seed dispersal through terpene-associated chemical cues. Ant-mediated dispersal (myrmecochory) involves seeds bearing lipid-rich elaiosomes that may contain terpenoid components attractive to foraging ants. Although the precise role of terpenes remains under investigation, they are believed to enhance seed detection and transport (Wu *et al*., 2024).

A striking example of terpene-mediated specificity is observed in the fig–wasp mutualism (*Ficus hispida–Ceratosolen solmsi marchali*), where wasp attraction depends on both terpene composition and concentration during specific floral developmental stages (Câmara *et al*., 2024).

11.2: Role of Terpenes in Protection against Biotic and Abiotic Stress

Plants are continuously exposed to biotic stresses (pathogens, herbivores) and abiotic stresses (drought, salinity, heat). Terpenes contribute significantly to stress tolerance by functioning as chemical defenses, antioxidants, and signaling molecules (Tholl, 2015). Major crops such as rice, wheat, maize, and barley suffer substantial yield losses due to combined biotic and abiotic stressors, which are further intensified by climate change. Constitutive terpene emissions from glandular trichomes, as observed in tomato, provide baseline defense, while inducible terpene biosynthesis enhances stress-responsive protection (Câmara *et al*., 2024).

12: Other Applications of Terpenes

12.1: Pharmaceutical and Medicinal Applications

Terpenoids are extensively used in pharmaceutical research due to their anticancer, anti-inflammatory, antimicrobial, and neuroactive properties (Newman & Cragg, 2020). Clinically significant examples include paclitaxel (Taxol**)** from *Taxus* spp. and β-elemene from *Curcuma wenyujin*, both widely used in cancer therapy (Xiao, 2018). Monoterpenes such as menthol, limonene, and menthone exhibit anesthetic, bronchodilatory, and anti-inflammatory effects, supporting their widespread medicinal use (Chen, 2022; Yang, 2020; Tetali, 2019) (Table 10).

12.2: Food Industry Applications

Terpenes such as α-pinene, limonene, linalool, and geraniol are widely employed as natural flavoring agents and preservatives due to their pleasant aroma and antimicrobial properties (Gutiérrez-Del-Río *et al*., 2021; Triaux *et al*., 2021). Citrus-derived terpenes and eucalyptus oils are increasingly used in food preservation, particularly in dairy and bakery products (Belewu *et al*., 2012) (Table 11).

12.3: Cosmetic Applications

Terpenes and carotenoids are central to the cosmetics and perfumery industries owing to their fragrance, antioxidant activity, and skin-protective effects (Table 12). Compounds such as limonene, linalool, and patchoulol are widely incorporated into skincare and personal care products to prevent photoaging and oxidative damage (Shahidi, 2016; Grether-Beck, 2017**)**

13: Future Perspectives and Challenges

Advances in metabolic engineering and synthetic biology offer promising avenues for sustainable terpene production. Engineered microorganisms (*E. coli*, *Saccharomyces cerevisiae*) have already been employed for large scale synthesis of high-value terpenoids such as artemisinin and paclitaxel (Khanam *et al*., 2022). Emerging concepts such as non-canonical terpene biosynthesis and hybrid synthetic–biological approaches expand chemical diversity and may yield novel bioactivities (Ma *et al*., 2024). However, challenges remain, including low natural abundance, poor bioavailability, limited clinical translation, and regulatory constraints.

Conflict of Interest: The authors declare no conflicts of interest.

Declaration: AI tools were used to generate Figures.

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Table 10: summarizes representative terpenes, their pharmaceutical applications, and mechanisms of action.

Terpene	Class	Major Pharmaceutical Applications	Primary Mechanisms of Action	Key References
Paclitaxel (Taxol®)	Diterpene	Anticancer (breast, ovarian, lung cancers)	Stabilizes microtubules, inhibits mitotic spindle disassembly, induces apoptosis	Kingston, 2007; Newman & Cragg, 2020
β-Elemene	Sesquiterpene	Antitumor (lung, nasopharyngeal carcinoma), anti-inflammatory	Induces apoptosis, suppresses cell proliferation, modulates NF-κB and PI3K/Akt pathways	Xiao, 2018; Bai *et al*., 2019
D-Limonene	Monoterpene	Gastroprotective, anticancer (chemopreventive), antimicrobial	Induces phase I and II detoxifying enzymes, disrupts microbial membranes, modulates Ras signaling	Mukhtar *et al*., 2018; Tetali, 2019
Menthol	Monoterpene alcohol	Analgesic, antipruritic, local anesthetic	Activates TRPM8 cold receptors, modulates ion channels, reduces neuronal excitability	Yang, 2020
Linalool	Monoterpene alcohol	Sedative, anxiolytic, neuroprotective	Modulates GABAergic and glutamatergic neurotransmission, antioxidant effects	Gao *et al*., 2018
Geraniol	Monoterpene alcohol	Antimicrobial, anticancer, skin therapeutics	Disrupts microbial membranes, induces oxidative stress in cancer cells, anti-inflammatory	Battilana *et al*., 2011; Hao *et al*., 2021
β-Caryophyllene	Sesquiterpene	Anti-inflammatory, analgesic, gastrointestinal disorders	Selective CB2 receptor agonist, reduces oxidative stress and cytokine production	Sun *et al*., 2022
α-Pinene	Monoterpene	Anti-inflammatory, bronchodilator, antimicrobial	Modulates inflammatory mediators, inhibits microbial growth, improves airway function	Luo *et al*., 2006; Yuan *et al*., 2015
Artemisinin	Sesquiterpene lactone	Antimalarial, anticancer (experimental)	Generates reactive oxygen species via endoperoxide bridge, damages parasite proteins	Newman & Cragg, 2020; Khanam *et al*., 2022

Table 11: Application of terpenes in Food industry

Plant	Type of Terpene	Uses	References
Citrus fruits, vegetables, and spices	Terpenes like linalool, α-pinene, limonene, and geraniol (monoterpene)	Used as natural flavoring agents in the food industry flavoring additive in chewing bubble, candy, beverages, and many other products	(Gutiérrez-Del-río *et al*., 2021)
Chrysanthemum morifolium.	α-cucurmene,	Microbicidal activity, potential as a preservative in food processing	Kuang *et al*., 2018
Eucalyptus globulus. Lemmon grass	Eucalyptus oil (Limonene, *γ*-Terpenes) and Lemongrass oil(monoterpenes)	Preservation of soft cheese	(Belewu *et al*., 2012)

Table 12: Terpene Application in Cosmetics

Product	Plant	Terpene Type/ Chemical	Uses	Reference
Citrus oil	Lemon, Grapefruit	Monoterpene	Skin health improved, prevention of lifestyle-related skin diseases	(Bertuzzi *et al*., 2013)
Mint oil	Pappermint	Menthol Menthone	relieve skin irritation, sunburn, used in perfumery and as a flavour agent	(Kiełtyka-Dadasiewicz & Kubat-Sikorska, 2018)
Oil of Cedar	Cedrus deodara	Limonene, Cedrene, Pinene	Cosmetic, soap and perfume Industries.	Kumar, 2019
Floral Essential oils	Rose *Pogostemon cablin*	Limonene sesquiterpene compound known as patchoulol	Perfumery skin care treatments	(Nandhini *et al*., 2025)

Authors Contribution: Conceptualization and supervision, AM; writing original draft preparation, AB; writing review and editing, T, AA, JN; validation, MA, KS; assisted with literature screening, SF, AA, EF, IU, NH, MS, FS. All authors have read and agreed to the published version of the manuscript.

Funding: No funding is available for this article.

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