

REVIEW ARTICLE





Terpenes: Multifunctional roles for plant survival and sustainable farming

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Abstract

Terpenes are the largest class of plant secondary metabolites which play a major role in plant-environmental interactions and serve vital ecological and agricultural functions. Their volatile nature plays a crucial role in pollination and insect attraction by emitting chemical signals that lure pollinators and seed dispersers, while simultaneously repelling herbivores and attracting the predators of the pests. Terpenes exhibit strong antimicrobial and antiviral activities, making them highly effective against pathogens. The insecticidal activity of terpenes offers an effective and eco-friendly alternative to synthetic pesticides, helping to kill pests in an environmentally sustainable manner. Allelopathic interactions of terpenes suppress the germination and growth of weeds and offer sustainable weed management. Besides, terpene biosynthesis in plants is influenced by abiotic stresses such as drought, elevated temperature, light stress and UV radiation highlighting the critical role in defense and adaptation mechanisms in relation to environmental changes. β -caryophyllene, a sesquiterpene is crucial for pollination, pest management, pathogen resistance, allelopathy and stress tolerance, enhancing survival and sustainability of plants. Modulation of terpene levels due to climate change emphasize their role in improving plant resilience to changing environments. The involvement of terpenes in diverse biotic and abiotic interactions underscores the need for continued research to harness their sustainable applications in agriculture, ecology and beyond.

Keywords: abiotic stress; allelopathy; β -caryophyllene; pathogens; pollination; terpenes

Introduction

Terpenes are the natural compounds produced by plants, with more than 30000 distinct structures and serving as an essential building blocks in numerous biological and ecological processes. Terpenes and their oxygenated compounds are the major constituents of essential oils, playing pivotal roles in regulating cell growth and maintaining membrane fluidity and permeability (1). In addition to their physiological roles, terpenes perform multifunctional ecological roles including attracting pollinators, repelling herbivores, acting as natural insecticides and suppressing weed growth.

Field pests are often managed using synthetic insecticides, which pose significant risks to human health, the environment and other non-target species. The overuse of these chemicals disrupts the ecosystem by leaving behind harmful residues. This has driven a search for safe, natural alternatives such as terpenes found in essential oils (2). As ecofriendly insecticides, terpenes are naturally synthesized by the plants help to repel herbivorous insects and playing an important role in ecological pest regulation (3). Unlike synthetic insecticides, terpenes are biodegradable, leaves no toxic residues and degrade rapidly in the environment. Their application in the integrated pest management offers a

sustainable and long-term solution for agricultural pest control (4).

Pollination in plants is often hindered by habitat fragmentation, loss of foraging resources and the decline of pollinators. These limitations can cause failure in seed production, adaptability of plant species and long-term survival (5). Floral scent comprising terpenoids and aromatics are crucial for attracting pollinators. These volatile profiles vary across plant species and even in the same species at different times of day, a challenge for the recognition of pollinators (6). However, higher emissions of terpenoids have been shown to correlate with increased seed health, indicating that these compounds directly influence reproductive success by attracting pollinators (7).

Weeds pose significant threats to the crops by competing for resources like light, nutrients, water and space leading to the reduced growth and yield of crops. Additionally, weeds serves as a host for various pests and pathogens (8). The indiscriminate use of herbicides resulted in herbicide-resistant weeds causing environmental issues such as contamination of groundwater and ecosystem disruption and degradation of soil health. This has raised public awareness of health risks associated with herbicide overuse to the humans, animals and

the environment (9). The allelochemical activity of terpenes act as a sustainable alternative for weed control. By suppressing weed germination and growth, terpenes act as natural herbicides and replace synthetic herbicides. Thus, forms a promising tool for sustainable weed management (10).

Pathogens such as bacteria, fungi, virus and mycoplasma impact crop health and reducing the yield productivity. These pathogens interrupt the regular physiological and metabolic processes of plants. Terpenes inhibit the pathogenic microorganisms which pose a serious threat to the plant survival (11). Plants have evolved to produce antimicrobial compounds like terpenes that inhibit the growth of pathogenic microorganisms by blocking bacterial DNA synthesis, inhibiting biofilm formation and maintaining membrane integrity (12). The presence of these bioactive metabolites not only helps in the growth of plants but also helps for the plants in adapting to the pathogenic attacks (13).

Temperature stress, whether due to extreme heat or cold, adversely affects the plant growth and metabolism. High temperature causes cellular disruption, protein denaturation, lipid liquefaction and membrane damage, while cold stress alters membrane lipids, leading to a gel like consistency that restricts membrane functionality (14). UV-B radiation induces oxidative stress and cellular damage, reducing protein content and overall cellular function (15). Terpenes play a vital role in mitigating these stresses by stabilizing membranes, reducing proton leakage and maintaining cellular integrity, which helps in protecting cell structures and chloroplasts. In high-light

conditions, terpenes protect the photosynthetic machinery from photo-oxidative damage, enhancing the plant's resilience against light stress (16). Additionally, terpenes scavenge ROS during UV-B radiation stress, helping to maintain protein content and cellular function (15). Terpenes possess therapeutic attributes such as antifungal, antiviral, antihyperglycemic, analgesic, anti-inflammatory and antiparasitic effects contributing to disease prevention, immune system support and overall well-being (17). Through genetic engineering, plant derived terpenes can be refined into biofuels, reducing reliance on fossil fuels and lowering carbon emissions (17). Their antioxidant and anti-inflammatory properties make them valuable in the cosmetic industry, particularly in skincare, perfumes and therapeutic cosmetics (18). This review explores the diverse and multifunctional roles of terpenes, emphasizing their potential in agriculture and ecological resilience (Fig. 1).

Biosynthetic pathways of terpenes

The biosynthetic pathways responsible for terpenoid production include the mevalonate (MVA) pathway and methylerythritol phosphate (MEP) pathway (Fig. 2). These pathways produce essential isoprenoid precursors, isopentenyl pyrophosphate (IPP) and dimethylallyl pyrophosphate (DMAPP), which serve as building blocks for various terpenoids (17).

The MVA pathway begins with Acetyl-CoA condensation. Acetyl-CoA acetyltransferase catalyzes the formation of acetoacetyl-CoA, which is then converted into HMG-CoA by HMG-CoA Synthase (18). The rate-limiting step of this pathway involves HMG-CoA reductase, which reduces HMG

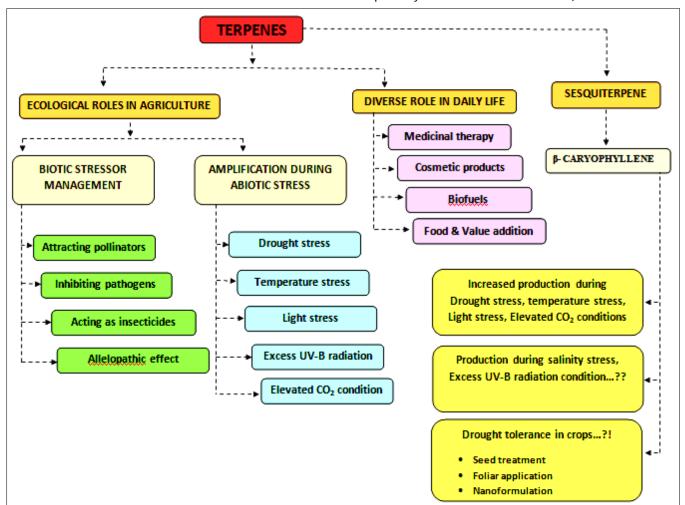


Fig. 1. Multifunctional role of terpenes.

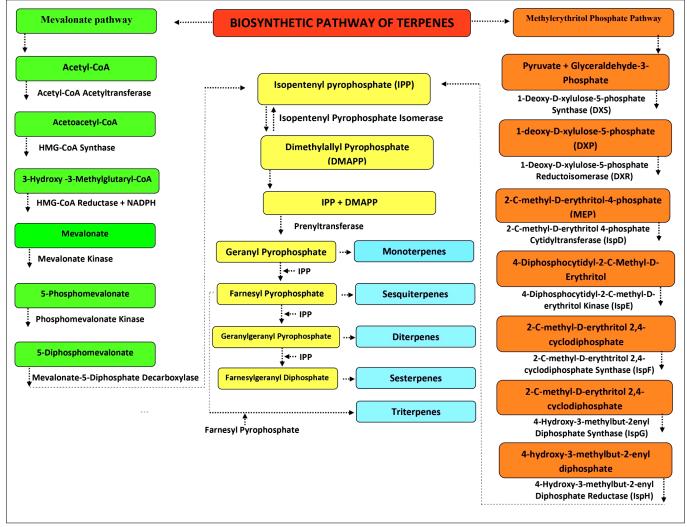


Fig. 2. Biosynthetic pathways responsible for terpenoid production.

-CoA to mevalonate using NADPH. Mevalonate undergoes sequential phosphorylation by mevalonate kinase and phosphomevalonate kinase to form 5-diphosphomevalonate (19). Mevalonate-5-diphosphate decarboxylase then converts this intermediate to IPP, releasing $\rm CO_2$. Isopentenyl Pyrophosphate Isomerase catalyzes the isomerization of IPP to DMAPP (20).

The MEP pathway, located in the plastids of plants and many bacteria, begins with the condensation of pyruvate and glyceraldehyde-3-phosphate. This reaction, catalyzed by 1-Deoxy-D-xylulose-5-phosphate Synthetase (DXS), produces 1-deoxy-D-xylulose-5-phos-phate (DXP), which is subsequently converted by 1-Deoxy-D-xylulose-5-phosphate reductoisomerase (DXR) into 2-C-methyl-D-erythritol-4-phosphate (MEP) (17). A series of enzymatic steps then lead to the formation of 4-hydroxy-3-methylbut-2-enyl diphosphate, which is finally reduced to both IPP and DMAPP (21, 22).

DMAPP and IPP condense to form geranyl pyrophosphate (GPP, C10), a precursor for monoterpenes (21). GPP condenses with IPP to form farnesyl pyrophosphate (FPP, C15), which serves as a precursor for sesquiterpenes (22). FPP undergoes further condensation with IPP to form geranylgeranyl diphosphate (GGPP, C20), leading to diterpenes (23). Additional condensation reactions result in the formation of sesterterpenes (C25), triterpenes (C30) and tetraterpenes (C40) (24).

Role of terpenes in pollinator attraction

Pollinators such as bees, butterflies, moths, flies and birds facilitate cross-pollination by transferring pollen from the anther to the stigma, drawn by the colors and fragrances of flowers (25). Lilac aldehyde, the main monoterpene of White campion, *Silene latifolia* attracts noctuid moth, *Hadena bicruris* (26). In Pineapple zamia (*Macrozamia lucida*), obligate pollination mutualism with *Cycadothrips* involves thermogenic male cones release β -myrcene, β -ocimene and allo-ocimene which prompt thrips to transfer pollinaria to female cones (27). Similarly, the fig wasp, *Ceratosolen solmsi marchali* is attracted to the receptive flowers of *Ficus hispida*, which emit monoterpenes such as linalool, limonene and β -pinene to lurepollinators (28).

Monkey flowers (*Mimulus lewisii*) use D-limonene, β -myrcene and E- β -ocimene to attract bumblebees (*Bombus* spp.) (29), while sweet rocket (*Hesperis matronalis*) emits linalool and β -ocimene to lure syrphid flies (6). Radiator plant (*Peperomia macrostachya*) releases geranyl linalool to attract arboreal ants (*Camponatus femoratus*) for seed dispersal (30). *Citrus reticulata* and *Citrus limon* with linalool are highly attractive to *Tetragonula laeviceps* (31).

Lavendar oil, rich in linalool and linalyl acetate, attracts honeybees for pollination and enhances oil quality. Pollinated lavender plants exhibit higher levels of these compounds compared to non-pollinated ones (32). *Philodendron fragmentissimum* secretes (Z)-jasmone to attract *Cyclocephala*

simulatrix Hohne for pollination (33). *Tetragonula angustula* is attracted to terpenes emitted by *Piper mollicomum* Kunth, which exhibits higher linalool concentrations during the flowering stage, with levels decreasing during fruiting (34).

Manihot violacea secrets geraniol and limonene to attract stingless bees (Partamona cupira), while Manihot oligantha emits myrcene and pinene to lure kleptoparasitic flies of Chloropidae family (35). Nicotiana attenuate releases (E)-β-ocimene and (E)-α- bergamotene to attract its pollinator Manduca sexta (36). Unpollinated flowers of Ficus carica emit more volatile organic compounds, including β-citral and geranial, attracting black fig fly, Silba adipate (37). Citrus mangshanensis produces high levels of β-myrcene, attracting bees (38). During blooming, Lavandula angustifolia increases the emission of (+)-R-limonene, β-trans-ocimene, linalool and linalyl acetate, attracting Apis mellifera, Apis cerana and other pollinators such as Macroglossum pyrrhosticum, Pieris rapae, Sarcophaga spp. and Calliphora vicina (39). The various terpenes involved in attracting pollinators are listed in Table 1.

Antimicrobial properties of terpenes against plant pathogens

Terpenoids provide resistance to various microorganisms by inhibiting their metabolic actions and eliminating them from plants by employing various mechanisms. Bacterial strains such as *Enterobacter aerogenes*, *Acinetobacter baumannii*, *Pseudomonas aeruginosa* are susceptible to antibiotics which are enhanced by geraniol (47). When geraniol is combined with an efflux pump inhibitor such as phenylalanine-arginine naphthylamide (PAN), it renders the organism fully susceptible to chloramphenicol, completely reversing its initial resistance (47).

Thymol and (+)-menthol exhibit antimicrobial activity against *Staphylococcus aureus* ATCC 6538P and *Escherichia coli* ATCC 15221 by exhibiting strong membrane disrupting effects on liposomes. But, linalyl acetate shows less detrimental effects on *Staphylococcus aureus* ATCC 6538P and *Escherichia coli* ATCC 15221 (48). Menthol possessing higher relative lipophilicity (Rm) values have the ability to penetrate lipid membranes and thereby shows the antimicrobial activity against pathogens (48).

Thymol and carvacrol make the cell membranes more permeable by increasing the NPN (N-Phenyl-1-naphthylamine) uptake. They effectively inhibit *E. coli* and *Salmonella typhimurium*. They make bacteria more sensitive to detergents like SDS and triton X-100 (49). Thymol and carvacrol reduce the viral inoculum of Tobacco Mosaic Virus (TMV) and Cucumber Mosaic Virus (CMV) (50). α -Terpinene, γ -Terpinene and α -Pinene shows the complete eradication of Herpes Simplex Virus Type 1 (HSV-1) (51).

Xanthorrhizol, a sesquiterpene acts against *Streptococcus mutans* by reducing its adherence to the cells. This mode of action reduces the adhesion phase of bacteria which is critical for the dental plaque formation. Xanthorrhizol also effectively reduces the colony forming units of *Mycobacterium smegmatis* and prevents the bacterial adherence and biofilm formation (52). Salvipisone shows both the bacteriocidal and bacteriostatic activity. Salvipisone acts as

an antimicrobial agent against *S. aureus* and *S. epidermidis* (53). The terpenes possessing antimicrobial activities against plant pathogens are listed in Table 2.

Allelopathic interactions mediated by terpenes

Allelopathy is the process wherein plants release chemicals to affect the growth of neighbouring plants. Allelopathic plants suppress weed germination and growth through the release of compounds such as terpenes, offering a natural means of weed control. The triterpenoids in *Praxelis clematide* are identified by colour changes such as brown, red or purple in the visible light and also under UV with the use of Liebermann-Burchard reagent (53). These compounds act as bioherbicides against *Asystasia gangetica* (54). The allelopathic activity exhibited by wheat against redroot pigweed demonstrates the suppression effect of terpenes such as linalool, borneol, terpinen-4-ol, linalyl acetate, geraniol and thymol (55).

The inoculation of *Solanum nigrum* with *Rhizoglomus intraradices* have resulted in the increased terpenoid levels in its fruits. The association of *Ipomoea purpurea* with *Funneliformis mosseae* showed enhanced terpenoid content in its flowers, which is likely inhibiting root or seedling growth in competing vegetation. When *Digitaria sanguinalis* got associated with both *F. mosseae* and *R. intraradices*, it showed limited allelopathic potential from the terpenoids in its seeds (56). The aqueous extract of fleagrass (*Adenosma buchneroides Bonati*) contains terpenoids such as ursolic acid and asiatic acid, which inhibit the germination and seedling growth of weed species including *Bidens pilosa*, *Boehmeria japonica* and *Pseudodonia thunbergii* (57).

The aqueous extract and powdered form of *Solanum linnaeanum* contain terpenoids such as cis- geranylacetone, trans- β -ionone and linalool oxide, which inhibit the germination and growth of *Lolium multiflorum*, *Sinapis alba* and *Trifolium incarnatum* (58). *Mikania micrantha* which possesses terpenoids such as α -terpineol, β -ocimene, β -myrcene and α -pinene, exhibits allelopathic effects against *Bidens pilosa* by reducing its germination rate, shoot and root length and chlorophyll content (59). *Parthenium hysterophorus* shows allelopathic effects on *Cyperus iria* through terpenoids including parthenin, dehydroleucodine, rishitin, gaillardilin and hymenoxynin (60). The aqueous extract of *Artemesia vulgaris* contains 1,8-cineole and vulgarin, which acts as a potential bioherbicide for controlling *Amaranthus retroflexus* L. (61), a common weed in *Zea mays* cultivation (62).

The essential oil of Euphorbia mauritanica contains monoterpene hydrocarbons (limonene, α-Pinene), oxygenated monoterpenes (eucalyptol, camphor), sesqui-terpene hydrocarbons (y-muurolene, cadalene), oxygenated sesquiterpenes (hexahydrofarnesyl acetone, butylated hydroxytoluene), diterpene hydrocarbons (cembrene, kaur-16ene) and oxygenated hydrocarbons (verticiol), which exhibit allelopathic potential against Dactyloctenium aegyptium and Urospermum picroides (63). Rainfed cotton intercropped with pearl millet results in improved weed control due to the presence of terpenes such as squalene and neophytadiene, which exhibit alleopathic potential towards Echinochloa crusgalli, lettuce and leafy spurge (64). The terpenes involved in

Table 1. Terpenes produced by plants for attracting the pollinators

Terpene	Plant source	Pollinators	Reference
Lilac aldehyde	White campion	Hadean bicruris	(26)
β-Myrcene	Macrozamia lucida Mimulus lewisii	Cycadothrips chadwicki Bombus spp.	(27, 29)
	Macrozamia lucida	Cycadothrips chadwicki	(27)
	Ficus hispida	Ceratosolen solmsi marchali	(28)
	Hesperis matronalis	Syrphid flies	(29)
β-Ocimene	Mimulus lewisii	Bombus spp.	(29)
р-остепе	Lavandula angustifolia	Apis mellifera Apis cerana Macroglossum pynhostictum Pieris rapae Sarcophaga spp. Calliphora vicina	(40)
Allo-ocimene	Macrozamia lucida	Cycadothrips chadwicki	(27)
	Ficus hispida	Ceratosolen solmsi marchali	(28)
	Hesperis matronalis	Syrphid flies	(6)
	Peperomia macrostacya	Camponotus femoratus	(30)
Linalool	Citrus reticulate	Tetragonula laeviceps	(41)
<u> </u>	Piper mollicomum Kunth	Tetragonisca angustula	(34)
	Lavandula angustifolia	Apis mellifera, Apis cerana, Macroglossum pynhostictum, Pieris rapae, Sarcophaga spp, Calliphora vicina	(40)
	Ficus hispida	Ceratosolen solmsi marchali	(28)
Limonene	Mimulus lewisii	Bombus spp.	(29)
	Manihot violacea	Partamona cupira	(35)
D-Limonene	Mimulus lewisii	Bombus spp.	(29)
Geranyl linalool	Peperomia macrostachya	Camponotus femoratus	(30)
Linalyl acetate	Lavandula angustifolia	Apis mellifera, Apis cerana, Macroglossum pynhostictum, Pieris rapae, Sarcophaga spp. Calliphora vicina	(32) (42)
(Z)- Jasmone	Philodendron fragrantissimum	Cyclocephala simulatrix Hohne	(43)
Geraniol	Manihot violacea	Partamona cupira	(35)
Myrcene Pinene	Manihot oligantha	Kleptoparasitic flies	(35)
α -Humulene	Passiflora sexocellata	Colletus spp.	(44)
	Passiflora sexocellata	Colletus spp.	(41)
β -Caryophyllene	Salvia verticillata	Apis mellifera, Bombus lapidaries, Bombus terrestris, Bombus pascuorum	(45)
(E)-β-Ocimene (E)-α-Bergamotene	Nicotiana attenuata	Manduca sexta	(46)
β –Citral Geranial	Ficus carica	Silpa adipata	(37)
(+) –R-limonene β –Trans-Ocimene	Lavandula angustifolia	Apis mellifera, Apis cerana, Macroglossum pynhostictum, Pieris rapae, Sarcophaga spp., Calliphora vicina	(42)
Germacrene D	Salvia verticillata	Apis mellifera, Bombus lapidaries, Bombus terrestris, Bombus pascuorum	(45)

Table 2. Terpenes and their role in the inhibition of pathogenic microorganisms

Terpenoid	Pathogen	Mechanism of action	Minimum inhibitory concentration (MIC)	References
Geraniol	Enterobacter aerogenes	Enhances susceptibility to antibiotics; when combined with PAN, reverses resistance to chloramphenicol	1.02 mg/mL	(47)
	Staphylococcus aureus		0.31 mg/mL	(48)
Thymol	Tobacco mosaic virus (TMV)	Exhibits antimicrobial activity and disrupts membrane	1 mmol/L	
	Cucumber mosaic virus (CMV)		1 mmol/L	
(+)- Menthol	Escherichia coli	Higher lipophilicity, facilitating penetration of lipid membranes	2.50 mg/mL	(48)
Carvacrol	Escherichia coli	Increases cell membrane permeability;	3 mM	(49)
	Salmonella typhimurium	enhances sensitivity to detergents like ŚDS	1 mM	
α-Terpinene γ-Terpinene α-Pinene	Herpes Simplex Virus Type 1 (HSV-1)	Complete eradication of HSV-1 at low concentrations	25 µg/mL	(50)

Plant source	Terpenoids	Target species	Reference
Triticum aestivum	Linalool,		
	borneol,		(65)
	terpinen-4-ol,	Amaranthus retroflexus	
	linalyl acetate, geraniol,		
	thymol		
Adenosma buchneroides Bonati	Ursolic acid	Bidens pilosa, Boehmaria japonica,	(66)
-deliosilia bacililerolaes bollati	Asiatic acid	Pseudodonia thunbergii	(55)
Solanum linnaeanum	Cis-Geranylacetone, trans- β-ionone,		
Soldman linnacanam	linalool oxide		
	α-Terpineol,	Bidens pilosa	(59)
Mikania micrantha	α-Pinene,		
	β-Ocimene,		
	β-Myrcene		
Parthenium hysterophorus	Parthenin, dehydroleucidine, rishitin, gaillardilin, hymenoxynin	Cyperus iria	(60)
	α-Pinene,camphene, bicyclo(3,1,0)hexane, β-pinene,		
	myrcene, limonene,		
	eucalyptol,	Lalium paranna	
Litsea pungens	linalool,	Lolium perenne, Bidens pilosa	(67)
	citronellal,	Bidens pilosa	
	cis-verbenol,		
	α-terpineol,		
	neral,		
	β-caryophyllene, humulene, caryophyllene oxide		
	Limonene,		
	α-pinene,		
Combondin noncontenuis	eucalyptol,	Dactyloctenium aegyptium,	(63)
	camphor,		
Euphorbia mauritanica	cadalene, hexahydrofarnesyl acetone,	Urospermum picroides	(63)
	butylated hydroxytoluene, cembrene,		
	kaur-16-ene,		
	verticiol		
		Echinochloa crus-galli,	
Pennisetum glaucum	Squalene, neophytadiene	Lactuca sativa,	(64)
		Euphorbia esula	

weed suppression through allelopathic effects are listed in Table 3.

Terpenes as eco-friendly insecticides

Terpenes play a significant role in pest management due to their insecticidal and repellant properties. The monoterpenes pose a threat to the insect pests. Carvacrol shows strong toxicity towards *Helicoverpa armigera* and *Drosophila suzukii* (68, 69). *Chilo partellus* and *Bemisia tabaci* are effectively controlled by 1,8-cineole (70, 71), while linalool is effective against *Plutella xylostella* and *Ceratitis capitata* (72, 73). Thymol exhibits its efficacy against *Chilo partellus* (70).

In the category of triterpenes, swietenitin O shows significant insecticidal activity against *Achea janata* and *Spodoptera litura*, showcasing its potential as an ecofriendly pest control solution (74). Methyl angolensate causes a remarkable mortality rate in *Spodoptera frugiperda* indicating its effectiveness as pesticide (75). Khayasin effectively targets *Brontispa longissima*, demonstrating its potential in managing this pest species (76).

Among sesquiterpenes, 9β -hydroxy- 1β H, 11α H-guaia-4,10(14)-dien-12,8 α -olide exhibits potent insectcidal activity against *Plutella xylostella* and *Bradysia odoriphaga*, highlighting its potential in agricultural pest management (77). 6b-acetoxy-9 oxofuranoeremophilane/dehydrodecompostin

showed a notable selectivity index against *Myzus persicae*, indicating its potential as a targeted pest control agent (78). 6-hydroxyeuryopsin demonstrates effective feeding inhibition against *Leptinotarsa decemlineata*, suggesting its utility in reducing pest populations (79). Also, 10α -hydroxy-1-oxoeremophilia-7(13), 8(9)-dien-12,8-olide achieved high feeding inhibition in *S. littoris*, further supporting its role in pest management strategies (78). The various terpenes involved in controlling pests are listed in Table 4.

Adaptation to abiotic stress through terpenes

Plants respond to various abiotic stresses, such as extreme temperature, elevated CO_2 levels, light and UV radiation by increasing the emission of terpenes and terpenoids. This serves as an adaptive and protective mechanism against environmental stressors. Cold stress poses a problem of decreasing the membrane fluidity. At 0 °C, *Pyrus communis* L. emitted higher levels of farnesene showcasing the plants ability to adapt to cold stress (82). *Daucus carota* L. responded to a milder cold stress of 9 °C by enhancing α -terpinolene emission to adapt for cold tolerance (83). In *Daucus carota* L. the increased emission of β -farnesene, α -humulene, α -pinene and γ -terpinene at 21 °C (83) and in *Hypericum brasiliense*, increased production of betulinic acid in heat stress at 36 °C reflects the metabolic flexibility of plants in response to heat stress (84).

Elevated CO₂ concentrations influence the terpenoid emission across various plant species which is linked to the

Table 4. Insecticidal potential of terpenes

	Terpenes	Insect species	Activity	Reference
	Carvacrol	Helicoverpa armigera	LC ₅₀ = 51.5 µg mL ⁻¹	(68)
Monoterpenes		Drosophila suzukii	$LD_{50} = 1.30 \mu g male^{-1} fly$	(69)
	1,8-Cineole	Chilo partellus	$LD_{50} = 412.1 \mu g larva^{-1}$	(70)
		Bemisia tabaci	M = 91.2 % (1000 mg/L)	(71)
	Linalani	Plutella xylostella	$LC_{50} = 3.37 \text{ ppm}$	(80)
	Linalool	Ceratitis capitata	$LD_{50} = 10.37 \text{ nL male fly}^{-1}$	(73)
	Thymol	Chilo partellus	$LD_{50} = 189.7 \mu g larva^{-1}$	(70)
	Swietenitin O	Achaea janata	$LC_{50} = 0.65 \mu g/cm^2$	(74)
		Spodoptera litura	$LC_{50} = 0.75 \mu g/cm^2$	
	Methyl angolensate	Spodoptera frugiperda	40 % mortality at 50 mg kg ⁻¹	(75)
T-21	Khayasin	Brontispa longissima	$LC_{50} = 7.28 \mu g/mL$	(76)
Triterpenes	Piscidinol I	Achea janata	$LC_{50} = 40.83 \text{ mg/cm}^2$	
		Spodoptera litura	$LC_{50} = 46.55 \text{ mg/cm}^2$	(81)
	Piscidinol L	Achea janata	$LC_{50} = 20.00 \text{ mg/cm}^2$	
		Spodoptera litura	$LC_{50} = 22.02 \text{ mg/cm}^2$	
Sesquiterpenes	9 β -hydroxy-1 β H,11 α H-guaia-4,10(14)-dien-12,8 α -olide	Plutella xylostella	$EC_{50} = 19.84 \text{ mg/L}$	(77)
		Bradysia odoriphaga	$LD_{50} = 18.71 \text{ mg/L}$	(77)
	6b-Acetoxy-9-oxofuranoeremophilane/ Dehydrodecompostin	Myzus persicae	SI = 74 %	(78)
	6b-Tigloyl-9-oxofuranoeremophilane	, ,		(- /
	6-Hydroxyeuryopsin	Lautinatawa ndanandinanta	FI = 72.2 %	(79)
	1,10-Epoxy-6-hydroxyeuryopsin	Leptinotarsa decemlineata	FI = 83.9 %	
	10a-Hidroxy-1-oxoeremophila-7(13),8(9)- dien-12,8-olide	Spodoptera littoris	FI = > 80 %	(78)

EC=Effective concentration causing 50 % mortality, **SI** = Susceptibility Index, **FI**= Feeding Inhibition, **LD** = Dose causing 50 % mortality, **LC** = Concentration causing 50 % mortality, **M** = Mortality.

changes in plant metabolism and stress signaling. Under elevated CO₂, *Quercus ilex*, shows an increased emission of limonene and *Zingiber officinale* produced more gingerol, which is known for its antioxidant and stress-mitigating properties (85). The native and Bt. transgenic varieties of *Gossypium hirsutum* showed elevated production of gossypol under higher CO₂ levels, reflecting the plant's adaptive mechanism to changing environmental conditions (86).

Light induced the stress in plants due to its variable intensities and spectral composition influencing the production of terpenoids. Under high light conditions, *Fluorensia cernua*, showed an increased emission of camphene, α -thujene and limonene (16) while *Brassica juncea* L. showed an elevated production of α - and β -carotenes, violaxanthin and lutein, which contributed to enhanced photoprotection and stress adaptation (87).

UV-B radiation triggers the increment in the terpenoid content in plants and strengthens their natural defense systems. *Coleus forskohlii* and *Withania somnifera* Dunal exhibited increased emissions of β -carotene, with the latter also emitting higher levels of lycopene under UV-B, preventing the tissues from radiation induced damage (88, 89). *Zea mays* demonstrated enhanced emissions of β -carotene and lutein (90). These protective mechanisms show the role of terpenes in

mitigating abiotic stress by enhancing plant adaptation and tolerance. The terpenes involved in plant responses to various abiotic stresses are listed in Table 5.

β- Caryophyllene: A multifunctional terpene

β- Caryophyllene, a bicyclic sesquiterpene, is one of the twelve most common volatile compounds in floral scents, occurring in over 50 % of angiosperm families and present in many essential oils (93). Passiflora sexocellata G- caryophyllene and α -humulene to attract *Colletus* spp. for pollination (44). Salvia verticillata contains high levels of β- caryophyllene, germacrene D and bicyclegermacrene, which attract pollinators like Apis mellifera and several Bombus species (45). In maize, (E)- β -caryophyllene released by roots attracts the ento-mopathogenic nematode Heterorhabditis megidis, which kills pests like Galleria mellonella and Diabrotica virgifera. Maize leaves attacked by Spodoptera littoris emit β-caryophyllene, which attracts the parasitic wasp, Cotesia marginiventris thereby contributing to pest population control (94, 95). Genes encoding β-caryophyllene synthase, such as QHS1 in Artemisia annua, have been utilized for heterologous production of β-caryophyllene, which exhibited the inhibitory effects against pathogens such as Sclerotinia sclerotiorum and Fusarium oxysporum (96).

At low concentrations, β-caryophyllene promoted

Table 5. Role of plant-derived terpenes in adaptation to abiotic stresses

Abiotic stress	Plant	Terpenoids	Environmental conditions under which modulations in terpene concentrations are observed	References
Cold stress	Pyrus communis L.	Farnesene	0°C	(91)
	Daucus carota L.	α-Terpinolene	9 °C	(83)
	Hypericum brasiliense	Betulinic acid	36 °C	(84)
Heat stress	Daucus carota L.	β-Farnesene, α-Humulene, g-Terpinene, α-Pinene, ocimene, camphene, caryophyllene, β-Myrcene	21°C	(83)
	Quercus ilex L.	Limonene	700 ± 250 ppm of CO ₂	(92)
Elevated CO ₂	Zingiber officinale roscoe	Gingerol	800 ppm of CO ₂	(85)
	Gossypium hirsutum	Gossypol	750 μ l/L of CO ₂	(86)
Light stress	Flourensia cernua	Camphene, Tricyclene, α-Thujene, β-Pinene, myrcene, 1,8-cineole, Limonene, γ-Terpinene, trans-sabinene hydrate, bornyl acetate, caryophyllene oxide, β-Cubebene	70 μmol m ⁻² s ⁻¹ light condition	(16)
	Brassica juncea L. 'Red Lion'	α-Carotene,	100 μmol m² s ⁻¹ light condition	
	Brassica rapa var chinensis	β-Carotene, Violaxanthin,	440 μmol m² s ⁻¹ light condition	(87)
	Brassica rapa var. rosularis	Lutein/Zeaxanthin	330 μmol m² s ⁻¹ light condition	
UV-B radiation	Coleus forskohlii	β-carotene	UV-B radiation of 9.6 kJ m ⁻² d ⁻¹	(88)
	Withania somnifera Dunal	β-carotene Lycopene	UV-B radiation of 9.6 kJ m ⁻² d ⁻¹	(88)
	Zea mays	β-carotene Lutein	UV-B radiation of 8.35 kJ m ⁻² per day	(90)

growth in some plants, but at higher concentrations, it inhibited the germination and growth of species like *Amaranthus retroflexus* and *Echinochloa crus-galli. Mikania micrantha* emits β -caryophyllene, showing allelopathic effects on weeds like *Brassica campestris*, promoting growth at low concentrations but inhibiting germination at higher levels (97). Stress conditions like cold, drought and heat significantly increase β - caryo-phyllene production. In holy basil, cold stress and drought stress increased β -caryophyllene levels (98). Heat stress in *Polygonum minus* enhances emission of terpenoids like β -caryophyllene (14). Increased light intensity boosts β -caryophyllene emissions in *Citrus sinensis* (99). Under water stress, *Origanum vulgare* shows elevated β - caryo-phyllene levels (100).

Conclusion

Terpenes are the essential secondary metabolites that play diverse and beneficial roles in plant biology. The characteristic volatile nature enables them to create a communication signal, which is involved in direct defenses like deterring pests, attracting beneficial insects for pollination and indirect defences such as attracting predatory insects that reduce the population of pests. By eliminating the pest and pathogen community, terpenes strengthen the plants' resilience and eliminate the weed community by suppressing their growth through their allelopathic potential. Additionally, terpenes alleviate abiotic stresses, stabilizing the plant's cellular structures and modulating stress related processes. The terpenes will be used to enhance sustainable agricultural practices in future. Terpene-based biocontrol agents will reduce the need for synthetic pesticides and support the ecofriendly pest management. Crops can be genetically modified to produce higher amounts of terpenes thereby directly enhancing their resistance to pests and environmental stresses. Future research on terpenes should focus on developing crop varieties better suited to changing climatic conditions, while also contributing to the sustainability and resilience of agricultural ecosystems.

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Authors' contributions

SKJ conducted the literature review, drafted and edited the manuscript. NS and MD assisted in the final editing of the manuscript. GSK and SM performed plagiarism checking and made necessary corrections.

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