International Journal of Food Science and Nutrition
www.foodsciencejournal.com
ISSN: 2455-4898
Received: 09-05-2026, Accepted: 09-06-2026, Published: 24-06-2026
Volume 11, Issue 2, 2026, Page No. 292-304

Plant secondary metabolites and stress tolerance: A comprehensive review

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DOI: https://doi.org/10.66856/ijfsn.2026.11.2.11101

Abstract

Plant secondary metabolites play a crucial role in defending against various biotic and abiotic stresses. Based on their structure, these metabolites can be broadly classified into two main categories: nitrogen-containing and non-nitrogen-containing compounds. This includes a diverse range of phytochemicals such as glucosinolates, terpenes, alkaloids, terpenoids, flavonoids and phenolics. These tissue-specific metabolites accumulate at different stages of a plant's life cycle, depending on the plant's needs. Understanding the roles of these compounds under different stress conditions helps in studying their functional significance. In conclusion, recent research highlights the limitations of the current classification systems for plant metabolites. By viewing secondary metabolites as integrated parts of dynamic metabolic networks influenced by environmental stresses, we can gain deeper insights into plant metabolism.

Keywords: Biotic stress, abiotic stress, secondary metabolites, phenolics, flavonoids, terpenoids

Introduction

Secondary metabolites are compounds produced by plants that enhance their ability to survive and compete within their environment. These substances comprise a wide range of structurally diverse molecules, typically derived from primary metabolites or their biosynthetic intermediates. They include fragrances, flavors, pigments, natural pesticides and food additives with significant applications in agriculture, industry and pharmaceuticals. Plants are constantly exposed to various environmental stresses both abiotic and biotic that can limit their growth and agricultural productivity. For centuries, secondary metabolites have been recognized for their broad biological activities and have played a central role in traditional medicine. Today, they are considered valuable bioactive compounds used in pharmaceuticals, cosmetics, food additives, agrochemicals, insecticides, pigments and nutraceuticals. Recent studies show that in Western countries, where synthetic chemistry dominates pharmaceutical production, approximately 25% of drugs are derived from plant-based natural products **[1].** The plant kingdom, therefore, represents a vast, environmentally friendly source of complex chemicals. Although the chemical industry continues to invest in synthesizing these compounds, it often falls short of replicating their complexity and efficiency. Thus, secondary metabolites significantly contribute to the economic value and sustainability of plant resources.

The ability to synthesize secondary metabolites has been selected through the course of evolution in different plant lineage when such compounds address specific needs. Floral scent volatiles and pigments have evolved to attract insect pollinators and thus enhance fertilization. To synthesize toxic chemical has evolved to ward off pathogens and herbivores or to suppress the growth of neighboring plants. Some specific biomolecules serve cellular functions that are unique to the particular plant in which they occur. Numerous secondary metabolites are defense compounds that protect against biotic and abiotic stresses such as infection, predation, ultraviolet radiation and drought **[2].** Plant secondary metabolites have been described as being antibiotic, antifungal as well as antiviral and therefore able to protect plants from pathogens *i.e.*, phytoalexins and also anti-germinative or toxic for other plants. Besides, they constitute important UV absorbing compounds, thus preventing serious leaf damage from the light **[3].** This article reviews the classification of secondary metabolites that synthesize by plants as well as their biological functions and work as plant defense against abiotic and biotic stresses.

Classification of plant secondary metabolites

Plant secondary metabolites can be classified in two major groups i.e. [1] Nitrogen containing secondary metabolites. This group is further classified into five sub-groups *i.e.*, amines, non-proteinogenic amino acids, alkaloids, cyanogenic glycosides and glucosinolates and [2] non-Nitrogen-containing secondary metabolites, which can further be classified into four groups *i.e.*, Polyketides, Phenolics, Polyacetylenes and Terpenoids [Fig. 1].

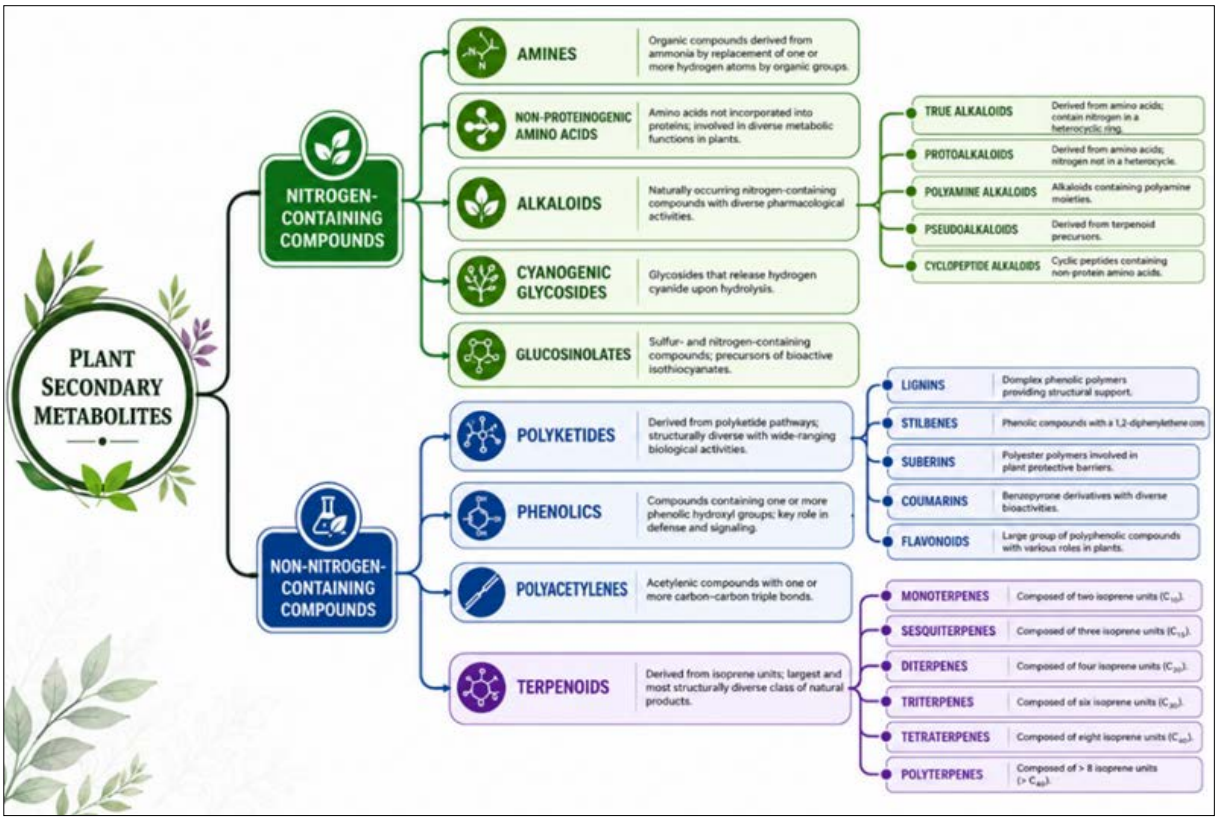


Fig 1: Classification of Plant Secondary Metabolites

Nitrogen containing plant secondary metabolites

Amines: They are low molecular weight nitrogen-containing compounds found in higher plants. It is formed from amino acids through processes such as decarboxylation or aldehyde transamination. These compounds often serve as precursors to various alkaloids. Among them, putrescine, spermidine and spermine are well-known polycationic amines that are universally present in living cells. Amines are essential for plant growth and development and their metabolic pathways are closely linked to the cell cycle **[4].** Beyond their role in plants, amines are crucial for sustaining life, as they contribute to the formation of amino acids which is fundamental building blocks of proteins in all organisms. In plants, amines also help defend against abiotic stresses such as drought and temperature extremes.

In industrial applications, many amines are used in products like pesticides and in processes such as leather tanning. Some amines, such as methamphetamines and amphetamines are known for their use as recreational drugs. Aniline, another type of amine plays a key role in the dye manufacturing industry. Additionally, serotonin a vital biological amine acts as a major neurotransmitter in the brain, regulating hunger and influencing overall brain function as well as processing speed.

Non-proteinogenic amino acids: They are amino acids that are either naturally occurring or chemically synthesized but are not directly encoded by the genetic code. They form a small group characterized by a central carbon atom bonded to an amino group, a carboxyl group, a side chain and an α-hydrogen in the *levorotatory* [L] configuration except in the cases of glycine and proline, which have unique structures. Examples of non-proteinogenic amino acids include β-alanine, γ-aminobutyric acid [GABA], δ-aminolaevulinic acid, D-alanine and D-glutamate.

These amino acids perform a wide variety of functions in plants and other organisms. They can act as deterrents to herbivores, antimicrobials, stress protectants, signaling molecules, nitrogen storage compounds and even as toxins to both invertebrates and vertebrates. Some also function as allelochemicals, which influence the growth of neighboring plants. In addition to their biological roles, non-proteinogenic amino acids are crucial in peptide and drug discovery. For instance, 3,4-dihydroxyphenylalanine [L-DOPA] is used in the treatment of Parkinson's disease and enalapril, a drug for high blood pressure, contains homophenylalanine [5].

These amino acids also participate in central metabolic processes, acting as intermediates in signaling pathways during plant stress responses. Examples include ornithine, citrulline, arginosuccinate, homoserine, homocysteine and cystathionine.

Alkaloids: Alkaloids are a diverse group of naturally occurring basic organic compounds that contain nitrogen and generally have low molecular weight. These compounds are primarily involved in plant defense, offering protection against herbivores and pathogens. Within plant cells, alkaloids can be found in various organelles, including mitochondria, vesicles, chloroplasts and vacuoles **[6].**

Alkaloids are typically classified into five main categories:

1. **True alkaloids:** These contain nitrogen within a heterocyclic ring and are derived from amino acids. Examples include *atropine*, *nicotine* and *morphine*.
2. **Proto alkaloids:** These also originate from amino acids but do not have nitrogen in a heterocyclic ring. Examples include *mescaline*, *adrenaline* and *ephedrine*.
3. **Polyamine alkaloids:** Derived from polyamines such as *putrescine*, *spermidine* and *spermine*.

4. **Pseudo alkaloids:** These resemble alkaloids but are not derived from amino acids. Notable examples include *caffeine*, *theobromine*, *theacrine* and *theophylline*.
5. **Cyclopeptide alkaloids:** These are macrocyclic compounds composed of a hydroxy styryl amine, an amino acid and a β-hydroxy amino acid with one or two additional substituent units attached to the ring.

Alkaloids often serve as chemical defenses due to their bitterness and toxicity. For instance, in potatoes, compounds like α-solanine and α-chaconine are toxic to larvae of the Guatemalan potato moth, helping protect the tubers [7]. Alkaloids may also serve as nitrogen reserves in times of nitrogen deficiency and under certain conditions may act as growth regulators or alternate energy sources when carbon dioxide assimilation is limited.
Medicinally, alkaloids display a wide range of biological activities. They can act as analgesics, muscle relaxants, antiarrhythmics, stimulants and treatments for conditions such as Alzheimer's disease, glaucoma and various infections. Additionally, many alkaloids exhibit antibacterial, antiviral, insecticidal, antiproliferative and antimetastatic properties, showing promise in both *in vitro* and *in vivo* studies for cancer treatment [9].

Cyanogenic glycosides: They are plant secondary metabolites that contain a nitrile group and can release cyanide when broken down by enzymes. This breakdown typically occurs when the plant tissue is crushed, chewed, or processed, triggering a hydrolysis reaction that liberates cyanide.
These compounds are predominantly synthesized from six amino acids: valine, isoleucine, leucine, phenylalanine, tyrosine and cyclopentenyl glycine [a non-protein amino acid]. Common examples include:

- Linamarin, found in cassava, white clover and linseed
- Dhurrin, present in species of the sorghum genus
- Prunasin and amygdalin, found in fruits like apple, pear and cherry

Cyanogenic glycosides serve as chemical defense agents for plants as they release hydrogen cyanide [HCN], a potent toxin. Hydrogen cyanide interferes with cellular respiration by inhibiting the electron transport chain, specifically by binding to cytochrome oxidase, thereby blocking ATP production and proving lethal to most organisms [9].

Glucosinolates: Glucosinolates are nitrogen and Sulphur containing compounds derived from amino acids such as methionine, alanine, valine, leucine, phenylalanine, tyrosine and tryptophan mainly found in Brassica family. They are water soluble anions and belong to the glucosides. The central carbon atom of every glucosinolates sis bound to the sulfur atom of thioglucose group where a sulfate group binds via a nitrogen atom. In addition, the central carbonic bound to a side group; different glucosinolates have different side groups and it is varying in the side group that is responsible for the variation in the biological activities of these plant compounds. Glucosinolates are natural components of many pungent plants such as mustard, cabbage and horseradish. These natural chemicals most likely contribute to plant defense against pests and diseases and impart a characteristic bitter flavor property to cruciferous vegetables. The major role of glucosinolates in plants is believed to be responsive to external or environmental stimuli. They are involved in communicating and triggering a range of information pertaining to plant defense against insects, fungi and some food bacteria. Glucosinolates are heat unstable, so they are partially destroyed by cooking. Some most important of glucosinolates are erucin, glucobrassicin, glucosinalbin, glucoerucin, sinigrin and progoitrin.

Non-nitrogen containing plant secondary metabolites

Polyketides: Polyketides represent a large group of structurally diverse molecules among the plant secondary metabolites many of which have important industrial applications in the food and pharmaceutical industries. Polyketides are synthesized from one of three classes of enzymes differentiated by their biochemical features and product structure: type I, type II or type III polyketide synthases. They are usually biosynthesized through the decarboxylative condensation of malonyl-CoA derived extender units in a similar process to fatty acid synthesis. Some plant polyketides having anticancer, antimicrobial, antiviral, antioxidant, neuroprotective and estrogenic activities **[10].** They also used as potent pesticides. Different polyketides such as coronatine worked partly as a mimic of methyl jasmonate undergoing biological stress. Tabtoxin and phaseolotoxin are strongly antimicrobial and function by inhibiting glutamine synthetase and ornithine carbamoyl transferase, respectively. While, syringomycin and syringopeptin form pores in plasma membranes, a process that leads to electrolyte leakage **[11].**

Phenolics: Phenolics are chemical compounds that contain a hydroxyl group [-OH] directly attached to an aromatic hydrocarbon ring. They represent a chemically diverse group of secondary metabolites, with phenol being the simplest form. The majority of known phenolic compounds are derived from plants. Phenolics play crucial roles in plant defense, particularly under abiotic and biotic stress conditions largely due to their antioxidant properties. They are also important structural components of the plant cell wall, contributing to the formation of lignin, cutin and suberin which enhance mechanical strength and provide barriers against pathogens. In terms of defense, phenolics act as deterrents against herbivores and pathogens. Compounds such as simple phenolic acids, tannins and phenolic resins located on the plant surface discourage feeding. Flavonoids and anthocyanins contribute to the coloration of flowers and fruits, helping attract pollinators and animals for seed dispersal. When plants experience microbial attack, they accumulate low-molecular-weight phenolic compounds known as phytoalexins, which are part of the plant's active defense mechanisms. Among these, hydroxyl coumarins and hydroxyl cinnamate conjugates are particularly significant in disease resistance.
Some phenolics also exhibit allelopathic effects, influencing the growth of surrounding plants. A notable example is juglone, a toxic compound found in Juglans [walnut] species. Juglone is stored in a non-toxic glucoside form and becomes active through enzymatic conversion once released into the soil. Phenolics also function as signaling molecules in plant-microbe interactions. For instance, flavonoids secreted by leguminous plants trigger the expression of nodulation genes in symbiotic nitrogen-fixing rhizobia.

Additionally, salicylic acid is recognized as a key signaling compound that activates plant immune responses against a wide range of pathogens. Beyond their biological roles, polyphenolics are valued in food and industry. Their astringent taste contributes to the flavor of foods, wines and herbal teas. Historically, tannin-rich plants were used in the leather tanning industry. Furthermore, phenolic pigments like lycopene, anthocyanins and flavones are widespread as natural colorants in fruit juices, wines and jams.

Anthocyanins have considerable potential in the food industry as safe and effective food additives.

1. **Lignin:** They are a large group of low molecular weight polyphenols found in plants, particularly in seeds, whole grains and vegetables. Lignin are precursors to phytoestrogens play a role as antifeedants in the defense of seeds and plants against herbivores.

2. **Stilbenes:** They are hydroxylated derivatives from group of stilbenoids. Most stilbenoids are produced by plants. *i.e.,* Aglycone like pterostilbene in almonds, pine and vaccinium berries, resveratrol in grapes as well as glycosides astringe in in the bark of spruce and piceid is a resveratrol derivative in grape juices.

3. **Suberin:** Suberin is a lipophilic macromolecule found in specialized plant cell walls, wherever insulation or protection toward the surroundings is needed. Suberized cells form the periderm, the tissue that envelops secondary stems as part of the bark and develop as the sealing tissue after wounding or leaf abscission.

4. **Coumarins:** They are aromatic organic chemical compounds. It can be placed in the benzopyrone chemical class and considered as a lactone. It is a colorless crystalline solid with a sweet odor resembling the scent of vanilla and a bitter taste. It is found in many plants, where it may serve as a chemical defense against predators. By inhibiting synthesis of vitamin K, a related compound is used as the prescription drug warfare in, an anticoagulant which inhibits formation of blood clots, deep vein thrombosis and pulmonary embolism.

5. **Flavonoids:** They are a class of polyphenolic secondary metabolites consisting of two phenyl rings and a heterocyclic ring found in plants. Flavonoids are the most important plant pigments for flower coloration, producing yellow, red or blue pigmentation in petals designed to attract pollinator animals. In higher plants, flavonoids are involved in UV filtration, symbiotic nitrogen fixation and floral pigmentation. They may also act as chemical messengers, physiological regulators and cell cycle inhibitors. Over 5000 naturally occurring flavonoids have been characterized from various plants. They are classified as anthocyanidins, anthoxanthins, flavanones, flavanonols, flavans, isoflavonoids, etc.

Many phenolics showed antimicrobial, anti-inflammatory, antibacterial, antiviral, antifungal, antitumor, anti-anaphylactic, anti-mutagenic, choleretic and broncho dilatory actions. It also showed circulatory stimulant, rubefacient and analgesic activities. Phenol itself was the first antiseptic used in surgery [12]. Flavonoids are known for its anti-inflammatory and antiallergic effects, for antithrombotic and Vaso protective properties, for inhibition of tumor promotion and as a protective for the gastric mucosa.

Polyacetylenes*:* Polyacetylenes are low molecular weight compounds produced by plants as a response to abiotic or biotic stresses **[13].** About 2000[2] different polyacetylenes and biogenetically related substances were identified in 24 families of higher plants. Polyacetylenes are relatively unstable, chemically and biologically active compounds and present in fungi, microorganisms, marine invertebrates and other organisms except for plants. Acetylenes form distinct specialized group of chemically active natural compounds, which are biosynthesized in plants of unsaturated fatty acids. They are localized in various plant organs and can be found both individually and as a compound with carbohydrates, terpene, phenolic and other compounds. They exhibit anti-inflammatory, anti- coagulant, anti-bacterial, antituberculosis, anti-fungal, anti-viral, neuroprotective and neurotoxic activity.

Terpenoids: Terpenoids constitute a class of chemical compounds present in all living organisms. Terpenes and terpenoids are the primary constituents of the essential oils of many types of plants and flowers. Terpenoids are the largest group of secondary metabolites, sub grouped according to the number of five carbon units in their skeletons; *i.e.,* C_5 [hemi], C_{10} [mono] C_{15} [sesqui], C_{20} [di], C_{25}[sester], C_{30} [tri] and C_{40} [tetra] terpenoids. Plant derived volatile organic compounds in the terpenoid family are predominantly mono and sesquiterpenoids. The terpenoids can be play various roles which include hormones, components of electron transfer systems, protein modification agents, membrane fluidity determinants, antioxidants etc. Terpenoids are also used as chemical messengers. If the communication is between different parts of the same organism, the messenger is referred to as a hormone **[14].** Gibberellic acid is a hormone used by plants to control their rate of growth.

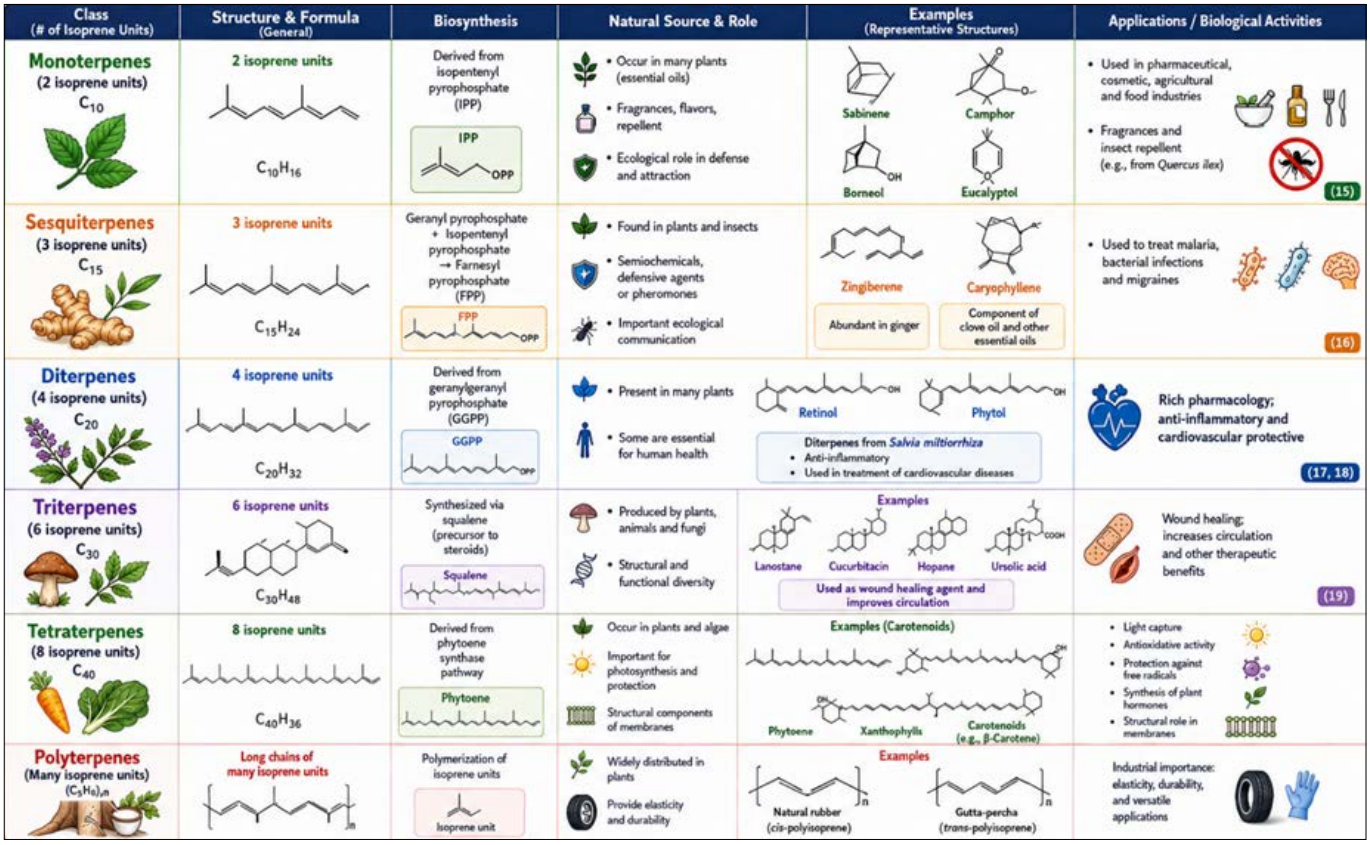
Secondary metabolites compartmentation in plant tissues

The spatial distribution of biocatalyst [enzymes] and biosynthetic products within and between cells is an important component of regulation for metabolic processes. Many metabolic processes in primary metabolism are compartmentalized, enabling the separation of incompatible and competing reactions and concentrating enzymes and metabolites. Secondary metabolites are widely distributed in various plants parts. Various scientists **[20-22]** have suggested that the various plant parts like cells, tissues and organs of

plants may possess different medicinal properties at different developmental stages in life cycle of plant and the developmental stages influence the initiation and then differentiation of particular cell structures involved in the biosynthesis and storage of secondary metabolites. Ma and Zhang [23] have noted that the plant growth and development are usually elicited or inhibited by different environmental conditions.

The adaptation of plant morphological, physiological, biochemical and biotechnological functions to the changes in biotic and abiotic stress condition may influence the accumulation of particular metabolites. The secondary metabolites pathways and their regulation are highly susceptible to environmental variations because the expression of genes involved in secondary metabolites pathways is altered by different stresses [24, 25].

Table 1: Classification, structure and biological importance of terpenes



Biosynthesis of secondary metabolites starts from basic pathways, *viz.*, and the glycolysis / shikimic acid pathways and subsequently diversifies, largely depending on cell type, developmental stage and environmental effects etc. Glycolysis takes place in the cytoplasm. The pyruvic acid is then further catabolized in the mitochondria to carbon dioxide and water with the release of ATP through the mitochondrial localized TCA cycle and the electron transport chain. Lastly, Calvin cycle enzymes are organized into a multienzyme complex, which appears to be loosely associated with thylakoid membranes near the sites of ATP and NADPH synthesis. The assembled complex results in enhanced activities of component enzymes such as Rubisco and may also play a role in the regulation of some pathway enzymes by light [26]. Plant secondary metabolites like terpenes have five carbon sisoterpenoid as their basic unit. It is provided in the form of dimethylallyl pyrophosphate and isopentenyl pyrophosphate, these are structural isomers to each other. These pair of building blocks are produced by two distinct metabolic pathways [1] the mevalonate pathway and [2] the non-mevalonate pathway. Phenolic compounds are synthesized from shikimic acid pathway. The nitrogen and sulfur containing compounds are mainly synthesized from the various amino acids. Secondary metabolites are hydrophilic/lipophilic compounds therefore need different cellular mechanism for their transport, storage and turnover. Most substances are synthesized in the cytoplasm, the endoplasmic reticulum or in the organelles. Hydrophilic secondary metabolites are usually stored in the vacuole and cytoplasm after their formation in cytoplasm, have to pass the tonoplast. The tonoplast is impermeable to many of the polar secondary metabolites whereas, lipophilic substances are sequestered in resin ducts, laticifers, glandular hairs, trichomes, thylakoid membranes or on the cuticle. The xylem or phloem work as transport routes but an apoplastic transport can also be involved. Storage can also be tissue and cell specific. Compartmentation of these compounds depends upon the protection providing to the plants [Fig. 2]. Alkaloids, terpenoids, amines, etc. are stored in chloroplasts. The tissue specific secondary metabolites accumulate at different stages of plant according to need of plant during its entire life cycle. In coffee plant, quinic acid is higher in seed at developmental stage than later stages; while in with *Withania somnifera* important economic part root contains with an olide and with ferin which are found higher during flowering stage in root, leaves and berries. In *Cinnamomum verum* plant, one year old leaves have higher content of eugenol compound and *Atropa belladonna* plant

contains hyoscyamine, amount of these secondary metabolites is found higher in four-year-old plant [Table 2]. Thus, synthesis of essential secondary metabolites is much specific according to stage and age of plant.

Table 2: Secondary metabolites accumulation in tissue and specific stages of plant development

Sr. No.	Secondary metabolite class	Metabolite name	Tissue	Stage	Plant name	References
1	Phenols	Cichoric acid	Root and rhizome	Fruiting stage	*Echinacea purpurea*	27
2	Phenols	Total phenol	Leaf	Vegetative and flowering stages	*Astragalus compactus* Lam.	28
3	Flavonoids	Flavonoids	Root	Full-bloom stage	*Scutellaria baicalensis* Georgi	29
4	Triterpene	Oleanolic acid and ecdysterone	Root	Vegetative growth period	*Achyranthes bidentata*	30
5	Flavonoids	Total flavonoids	Root	Whole growth stage	*Scutellaria baicalensis* Georgi	31
6	Triterpene	Saponin	Root	Older stage	*Panax notoginseng*	32
7	Oil	Essential oil	Stem bark	12 year old plants.	*Cinnamomum cassia*	33
8	Glycoside and flavonoids	Hyperin and quercetin	Bark	13-year-old plant	*Magnolia officinalis*	34
9	Terpenoids	Monoterpenes and sesquiterpenoids	First cotyledon	Flowering stage	*Melaleuca alternifolia*	35
10	Phenolic compound	Eugenol	Leaf	1-year-old leaf	*Cinnamomum verum*	36
11	Volatile oils	Volatile oils	Flower buds	Later stage	*Magnolia zenii*	37
12	Terpenes	Myrcene and ocimene	Mature flower buds	Flowering stage	*Antirrhinum majus*	38
13	Flavonoids	Chlorogenic acid and luteolin	Flower	Flowering stage	*Lonicera japonica* Thunb	39
14	Terpenoids	α-thujone, carene, β-pinene and γ-terpinene	Fruit	Fruiting stage	*Citrus medica* L.	40
15	Phenol	Quinic acid	Seed	Developmental stage of seeds	*Coffea*	41
16	Alkaloid	Aconitine	Root	Vegetative growth period	*Aconitum napellus*	42
17	Alkaloid	L-hyoscyamine	Foliage and berries	Four year old plant	*Atropa belladonna*	43
18	Alkaloid	Camptothecin	Bark and seeds	Young plant	*Camptotheca acuminata*	44
19	Alkaloid	Withaferin A withanolide	Root, stem, berries	Flowering stage	*Withania somnifera* (L.) Dunal	45
20	Anthraquinone glycoside	Aloin	Leaves	Flowering stage (18 month old)	*Aloe vera barbadensis*	46
21	Alkaloid	Vasicine	Leaves, bark, root bark, fruit	Developmental stage	*Adhatoda vasica* Nees.	47
22	Phenolic compounds	Thymol and carvacrol	Leaves	Whole life cycle	*Coleus aromaticus* Benth.	48
23	Terpenoids	Andrographolide	Aerial parts, roots or leaves	Flowering stage	*Andrographis paniculata*	49
24	Monoterpenoid and Phenyl propanoids	Linalool, methyl chavicol and Methyl eugenol	Leaves	Flower bud stage	*Ocimum basilicum* L.	50

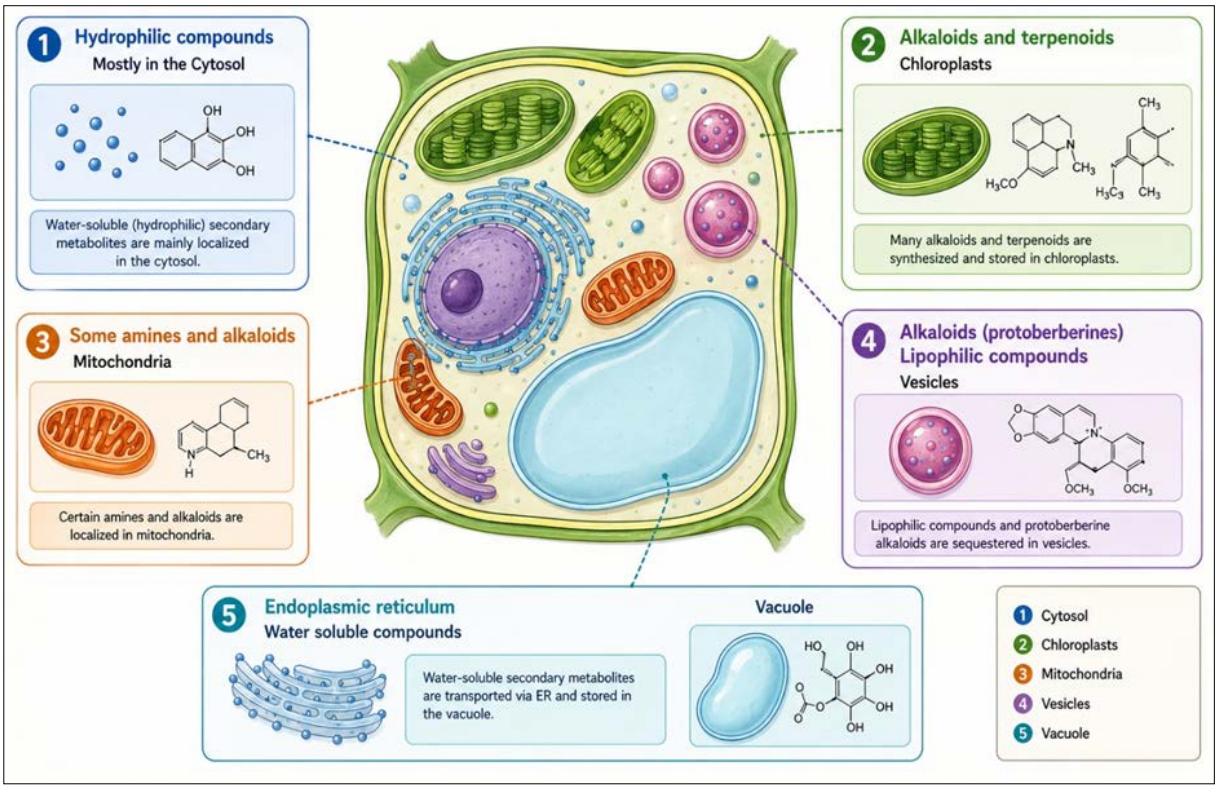


Fig 2: Intracellular compartmentalization of secondary metabolites in plant cells

Zaynab *et al.* [51] stated that the formation of secondary metabolites is the result of millions of years of plant's interaction with pathogens and it is considered that more than 1,00,000 metabolites are known to be involved in plant defense system, so the situation is still not clear. Although it is considered that plant with high concentration of secondary metabolites is more resistant to biotic and abiotic stresses but their production is thought to be expensive for plant growth and reproduction. Function and structure of plant secondary metabolites explain that why plants have evolved induced defense, which is characterized with increased concentration in various stress situations. The environmental stresses conferred to plants can be categorized in two types [1] abiotic stress which is the negative impact of non-living factor on the living organism in a specific environment and [2] biotic stress which is the result of damage done to plant by other living organisms such as bacteria, virus, fungi, beneficial and harmful insects.

Role of secondary metabolites in plant defense against abiotic stress

The accumulation, transport, distribution and specially synthesis of secondary metabolites are strictly influenced by the changing an environmental stress condition. Abiotic stress is responsible for the decrease of production and productivity of crop. During growth and development, plants interact with the various abiotic components such as water, light, temperature, soil and chemicals. Negative abiotic factors, such as water deficit stress or flooding, extremes of light and temperature and the presence of poor soil or toxic chemicals generate secondary stresses. These situations trigger variation in the biosynthesis of secondary metabolites. Thus, environmental factors are crucial determinants for the biosynthesis and fluctuations in plant secondary metabolites **[52].**

Irradiance with photons of different wavelengths and intensity is an essential abiotic component required by the plants for photosynthesis growth and secondary metabolic product accumulation. Plants require an appropriate intensity of light for photosynthesis and this affects the quality and accumulation of total alkaloids, terpenoids, flavonoids and phenolic acids. The effect of ultraviolet light exposure on secondary metabolites is common in medicinal plants [Table 3].

However, plant secondary metabolites have not been fully studied with respect to their relevant functions in plants under environmental stress. Low and high temperature ranges may have a negative impact on plant growth and development. Plants growing at elevated temperatures exhibit a decline in the photochemical efficiency of photosystem II, indicating stress enhancement. The biosynthesis of secondary metabolites is also associated with high temperature in plants. High-temperature stress usually increased the production of secondary metabolites, whereas some studies reported that secondary metabolites were decreased in plants under high-temperature stress. Thus, the secondary metabolites increase/decrease in response to elevated temperatures and this is dependent on the species and multiple factors. High temperature downregulates/upregulates the responding genes and affects the growth and development of plants. The content of flavonoids and phenolics is elevated under severe drought stress condition in plants. The enhancement of phenolic and flavonoid compounds is highly linked to the balance between carbohydrate sources and sinks. The accumulation of

Table 3: Plant secondary metabolites in defense against abiotic stresses

Sr. No.	Secondary Metabolites	Compound	Plant	Resistance Against	Abiotic Factor	Reference
1	Phenols	Anthocyanins, lignin, tannins	*Withania somnifera*	UV-B	Light	53
2	Phenols	Phenolic acids	*Chrysanthemum*	UV-B	Light	54
3	Phenols	Phenolic acids	*Astragalus compactus*	UV-B	Light	55
4	Phenols	Phenolic acids	*Arnica montana*	UV-B	Light	56
5	Phenols	Scutellarin	*Erigeron breviscapus*	Full sunlight	Light	57
6	Phenols	Flavonol quercetin-4'-O-monoglucoside	*Asparagus officinalis*	UV-B	Light	58
7	Alkaloids	Alkaloids	*Withania somnifera*	UV-B	Light	54
8	Terpenes	Sabinene, β-pinene, Borneol, Bornyl acetate, Z-jasmone	*Flourensia cernua*	50% shade	Light	59
9	Oil	Essential oil	*Mahonia breviracema*	Full sunlight	Light	60
10	Terpenes	Saponins	*Withania somnifera*	UV-B	Light	54
11	Sterols	Phytosterols	*Withania somnifera*	UVB	Light	54
12	Oil	Hexadecanoic acid	*Mahonia bodinieri*	50% Full sunlight	Light	60
13	Glucosinolate	Glucosinolate	*Nasturtium officinale*	UV	Light	61
14	Sesquiterpene lactone	Artemisinin	*Artemisia annua*	Pre-chilling	Temperature	62
15	Phenols	Phenolics	*Astragalus compactus*	High-temperature	Temperature	63
16	Phenols	Anthocyanins	*Chrysanthemum*	High temperature	Temperature	64
17	Fatty acid	α-Linolenic acid, jasmonic acid	*Camellia japonica*	Low temperature	Temperature	34
18	Phenols	Total phenolics	*Hypericum brasiliense*	Low water condition	Drought	65
19	Phenols	Total phenolics	*Trachyspermum ammi*	Low water condition	Drought	66
20	Phenols	Baicalin	*Scutellaria baicalensis*	Low water condition	Drought	67
21	Phenols	Rutin, Quercetin	*Hypericum brasiliense*	Low water condition	Drought	52
22	Phenols	Anthocyanins	*Labisia pumila*	Low water condition	Drought	68
23	Pentacyclic triterpenoid	Betulinic acid	*Hypericum brasiliense*	Low water condition	Drought	52
24	Sesquiterpene lactone	Artemisinin	*Artemisia*	Low water condition	Drought	52
25	Terpenes and flavonoids	Saponins, flavonoids	*Planta goovata*	Salinity stress	Salinity	69

Soluble carbohydrates in plant cells are affected by the reduced transport of soluble sugars under water deficit stress. When stresses act upon plants, changes in gene expression also take place. In low to moderate stress condition, the expression of many genes contributing in the synthesis pathway of secondary metabolite compounds are elevated and this requires high energy inputs.

Role of plant secondary metabolites in defense against biotic stress

Biotic stress occurs as a result of damage done to plant by other living organism *viz.*, bacteria, virus, fungi, beneficial and harmful insects. In order to defend themselves plants have developed a variety of defense responses many of which are induced by pathogen attack. In plants, secondary metabolites are present which are the byproduct of primary metabolic processes and does not have any direct effect on plant growth and development but acts as a defense mechanism in plants and they are considered as secondary metabolites. Secondary metabolites act as a plant defense system, along with this it is also a collector for many phytohormones which protect the plant against various types of stresses. The main primary function of secondary metabolites is to support the plant for growth and survival as well as help them to adapt to any harsh climate condition during the communication of pollination, legume root nodule and antagonistic interaction. During development stages of plants, different metabolic processes are going on like growth, genetic makeup etc which are the factors that determine production, type and concentrations of secondary metabolites. Basically, when the plants are exposed to various stress conditions then the secondary metabolites biosynthesis started. Plants are exposed to biotic stresses, the morphology and other phenolic pigments, activity of antioxidant levels, flavonoids, and phenol content altered by various stress conditions [70].

In plants defense system, widely distributed compounds are phenylpropanoids and flavonoids which possess different mode of action. Terpenes are toxins and deter herbivores. Antifungal drugs target major processes like cell signaling, physiological activities, enzyme inhibition, DNA alkylation and reproductive system etc. These compounds have hydroxyl group containing phenolics, which are likely to dissociate in phenolate ions. As phenolic hydroxyl groups form ionic bonds and hydrogen bonds with peptides and protons so, their higher number results in high astringency and denaturation. Protein properties are changed with any change in protein confirmation which can prevent crosstalk with other proteins and DNA/RNA. Secondary metabolites interact and changes three-dimensional structure of proteins by forming covalent bond with free sulfhydryl group. OH- or amino groups, resulting in loss of function or change in protein turnover. Walling [71] stated that secondary metabolites do not reduce the growth and development of plant instead they affect the fodder value of plant tissues where they are produced. During herbivory, α-glucosidase activated phytoanticipins results in release of biocidal aglycones. Hydrolyzation of glucosinolates by myrosinases during tissue disruption is classic example of phytoanticipins. Benzoxazinoids are another example of phytoanticipins that are present among *Poaceae*. During tissue damage, their hydrolysis by plastid targeted α-glucosidase produces biocidal aglycone.

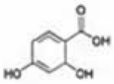
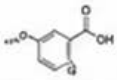
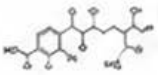
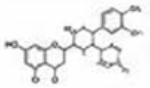
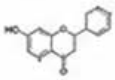
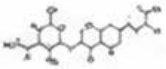
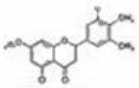
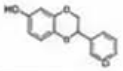
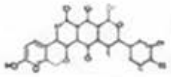
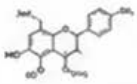
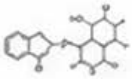
Benzoxazinoids that act as insect repellent. While, the phytoalexins include alkaloids, isoflavonoids, terpenoids, etc. affect the performance of herbivores.

Some plant secondary metabolites act as antimicrobial compounds like Tomatine. It activates monomeric G-protein pathways and phosphor tyrosine kinase [72] which binds to cell membrane followed by cell component leakage which leads to ROS burst and Ca^{+2} elevation in *Fusarium oxysporum*. Different Saponins show resistance against ever apathogenic fungi is produced in different plant species, while some of plant terpenes have industrial and medicinal importance [73]. Discovery of sesquiterpenoids phytoalexins, zealexins in F. *graminearum* infected maize was result of characterization of physiological responses. Zealexins showed resistance against *A. flavus* and *F. graminearum* [Table 4].

The various mechanisms such as physiological, biochemical and molecular metabolism are altered under stress condition in plant kingdom. Different secondary metabolites trigger in various plant parts depending on the stress condition occurring at various stages of plant and due to this reason various plants maybe rejuvenated. Some molecules participate in the construction of polymeric compounds to fight or invade pathogen penetration. Each plant has a sophisticated recognition system that enables rapid recognition of pathogen attack and according to this it can initiate a dynamic defensive response by signaling cascade [103]. There is a great association between biotic and abiotic stresses; this crosstalk regulated by transcription factors play an essential role in the stress response by directly regulating the expression levels of various stress- related genes. Various scientists [104, 105] have also reported that secondary metabolites play a promising role in adapting plants to their local environment. The regulatory mechanisms of vital plant secondary metabolites associated with plant must be studied further in detail. The cross talk between different metabolic pathways which are mainly regulated due to stress induced changes in plant defense system also need to be examined at various development stages.

Table 4: Plant secondary metabolites in defense against biotic stress

Sr. No.	Secondary metabolites	Compound	Plant	Resistance against (Organism)	Organism Type	Reference
1	Terpenoids	Limonene	Citrus	*Atta cephalotes*	Insect	[74]
2	Terpenoids	Monoterpenes	Pine and fir	Bark beetle	Insect	[75]
3	Steroids	Phytoecdysones	Common fern	Insect	Insect	[76]
4	Terpenoids	Trans anethole and thymol, citronellal	Tobacco	*Spodoptera litura*	Insect	[77]
5	Phenolics	Phenols	Wheat	*Phopalosiphum padi*	Insect	[78]
6	Phenolics	Phenols	Willow plant	*Galerucella linola*	Insect	[79]
7	Benzoic acid	Benzoic acid	Salix	*Operophtera brumata*	Insect	[80]
8	Phenolics	Phenolics	Strawberry	*Tetranychus urticae*	Insect	[81]
9	Phenolics	Gossypol	Cotton	*Heliothis virescens, Heliothis zea*	Insect	[82]
10	Alkaloids	Alkaloid demissine	Night shed potato	*Leptinotarsa decemlineata*	Insect	[83]
11	Benzoxazinoides	DIMBOA	Gramineae	*Ostrinia nubilalis*	Insect	[84]
12	Cyanogenic glycosides	Cyanogenic glycosides	Cassava	*Cyrtomenus bergi*	Insect	[85]
13	Cyanogenic glycosides	Amygdalin and prunasin	Bitter almonds plant	*Capnodis tenebronis*	Insect	[86]
14	Cyanogenic glycosides	Amygdalin and prunasin	Trifolium repens	*Hyperapostica*	Insect	[87]
15	Cyanogenic glycosides	Cyanogenic glycosides	Lotus	*Zygaena filipendulae*	Insect	[88]
16	Cyanogenic glycosides	Cyanogenic glycosides	*P. lunatus*	*Spodoptera eridania*	Insect	[89]

17	Aromatic aldehyde	Benzaldehyde 	Ornamental crops	*Botrytis cinerea*	Fungus	[90]
18	Phenolic compound	Protocatechuic acid 	Wheat	*Colletotrichum circinans*	Fungus	[91]
19	Phenolic compound	Salicylic acid 	Fruit and vegetable crop	*Eutypa lata*	Fungus	[92]
20	Phenolic compound	Vanillic acid 	Different crops	*Phytophthora infestans*	Fungus	[92]
21	Phenolic compound	Chlorogenic acid 	Tomato	*Fusarium oxysporum*	Fungus	[71]
22	Phenolic compound	Naringin 	Citrus aurantium	*Penicillium digitatum*	Fungus	[93]
23	Flavonoids	Flavones 	Legume seeds	*Aspergillus*	Fungus	[94]
24	Glycosides	Oleuropein 	Citrus aurantium fruit	*Phytophthora*	Fungus	[95]
25	Flavonoid	Nobiletin 	Different crops	*Phomatracheiphila*	Fungus	[96]
26	Flavonoid	Genistein 	Forest species	*Monilinia fructicola*	Fungus	[97]
27	Glycoside	Hordatin A 	Different crops	*Helminthosporium sativum*	Fungus	[98]
28	Alkaloid	7-deoxytrans-dihydronarciclasine 	Plantain lilies (Hosta plantaginea)	Tobacco Mossic Virus	Virus	[99]
29	Flavonoid	Bruceine-D 	*Brassica javanica*	Cabbage Mosaic Virus and Tobacco Mosaic Virus	Virus	[100]
30	Alkaloids	Quassinoid, β-carboline 	*Icarma quassioides*	Tobacco Mossic Virus	Virus	[101]
31	Alkaloids	7-demethoxytylophorine and 7-demethoxy-tylophorine N-oxide 	*Cynanchum komarovii*	Tobacco Mossic Virus	Virus	[102]

Conclusion

Plants constantly interact with the surrounding environment and they are constantly exposed to a number of adverse conditions. Biotic and abiotic stresses negatively affect the plant's growth and survival by altering the various physiological and biochemical mechanisms. The various types of stresses induce the oxidative and osmotic stresses in which reactive oxygen is formed and damages the biomolecules such as DNA, proteins, RNA, etc. and causes cell death. In order to minimize the impact of various stresses, plants produce diverse defense secondary metabolites such as phenolics, terpenoids, anthocyanins, etc. Thus, from the above discussion, it can be concluded that secondary metabolites are essential and prevent plants from any type of damage.

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