

METABOLIC DIVERSITY AND FUNCTIONAL ROLE OF SECONDARY METABOLITES IN FRUIT CROPS

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ABSTRACT

Fruit crops synthesize a diverse group of secondary metabolites, including phenolics, terpenoids and nitrogen-containing compounds, which play essential roles in plant growth, defence, fruit quality and human health. These metabolites contribute to resistance against biotic and abiotic stresses while influencing important organoleptic traits such as colour, flavour, aroma and nutritional value. Despite significant advances in fruit metabolomics, a comprehensive understanding of the metabolomic diversity, regulatory mechanisms, and integration of multi-omics approaches for fruit quality and stress resilience remains limited. This review summarizes the current knowledge on the metabolic diversity, classification, biosynthetic pathways, and regulatory mechanisms of secondary metabolites in fruit crops. It further discusses in metabolomics and integrated omics approaches, their application in breeding and crop improvement and future opportunities for developing nutritionally enriched and climate- resilient fruit cultivars.

KEYWORDS: Secondary Metabolites; Fruit Crops; Metabolic Diversity; Antioxidant; Crop Improvement

Abbreviations:

CV – Coefficient of Variation

ETI – Effector-Triggered Immunity

FLS – Flavonol Synthase

GC-MS – Gas Chromatography–Mass Spectrometry

GWAS – Genome-Wide Association Studies

HCN – Hydrogen Cyanide

IPP – Isopentenyl Diphosphate

LC-MS – Liquid Chromatography–Mass Spectrometry

MAS – Marker-Assisted Selection

MeJA – Methyl Jasmonate

MEP – 2-C-Methyl-D-Erythritol 4-Phosphate Pathway

MVA – Mevalonate Pathway

NMR – Nuclear Magnetic Resonance

PAL – Phenylalanine Ammonia-Lyase

PTI – Pattern-Triggered Immunity

QTL – Quantitative Trait Loci

SA – Salicylic Acid

STS – Stilbene Synthase

TPS – Terpene Synthase

UGT – UDP-glucose: Flavonoid 3-O-Glucosyltransferase

INTRODUCTION

Fruit plants create many different secondary metabolites to help them grow, survive, and produce high-yielding fruits. The majority of this group of compounds consists of phenols, terpenes (or terpenoids), and compounds that contain nitrogen. Secondary metabolites are important not only for protecting the plant from harmful environmental conditions and biological organisms, but also for providing desirable taste, colour, and aroma characteristics to harvested fruits (Sanchez-Ballesta et al., 2022; Tang et al., 2024). Secondary metabolites are widely recognized for their medicinal importance due to their anti-inflammatory, antioxidant and disease-preventing properties (Swallah et al., 2020). Advances in analytical techniques, including LC-MS, GC-MS, NMR, and 'omics', have allowed researchers to define fruit metabolomes and their regulatory networks with much greater detail than in previous research. However, the composition and concentration of metabolites vary greatly depending on the species, plant tissue developmental stages, and environmental conditions. (Commisso et al., 2021). Despite notable progress in metabolomic research, understanding the interaction between genetic regulation and environmental influences on secondary metabolite

accumulation remains limited. Effective crop improvement in fruit plants still depends on the integration of transcriptomics, proteomics, and metabolic approaches (Gu et al., 2024; Tohge et al., 2020). The objective of this review is to summarize the classification, metabolic diversity, biosynthesis regulation and functional significance of secondary metabolites in fruit crops with emphasis on phenolics, terpenoids and nitrogen-containing compounds. Literature published between 2010 and 2025 was collected from the databases Web of Science, Scopus, PubMed, and Google Scholar. The review focuses on metabolomics and integrated omics approaches associated with fruit quality, stress tolerance and crop improvement, whereas detailed medicinal and pharmaceutical applications are beyond its scope. In addition, modern analytical approaches and their potential application in crop improvement are discussed.

1. Classification of Secondary Metabolites in Fruits

Secondary metabolites, also called as specialized metabolites, are diverse natural compounds that are derived from primary metabolic pathways in tropical and subtropical fruit crops. (Kroymann, 2011) They are broadly classified into phenolics, terpenoids and nitrogen-containing compounds based on their chemical structure and biosynthetic origin (Pott et al., 2019)

1.1 Phenolic compound

Phenolic compound are diverse group of metabolites ranging from simple molecule to complex polymer, characterized by at least one aromatic ring with one hydroxyl group they are mainly synthesized through the shikimate and phenylpropanoid pathway (Tang et al., 2024). Based on structure, they include structures such as flavonoids, non-flavonoids, simple flavonoids and stilbenes as well as polymeric forms like tannins (Xu et al., 2025; Balasundram et al., 2006). Research on phenolics has increased due to raising interest in functional foods. With studies in grapes, apples and strawberries showing their strong influence on nutritional quality, storage and processing traits.

1.1.1 Flavonoids

In horticultural plants, including fruit crops, these are the most prevalent secondary metabolites. Flavonoids possess a C6-C3-C6 diphenylpropane structure consisting of two aromatic rings with a three-carbon linker. They are divided into flavonols (found in apples), flavones (found in oranges), flavanones (found almost exclusively in citrus fruits like lemons and oranges), anthocyanins (which give berries and grapes their red, blue, and purple pigments), isoflavones, flavanols, and chalcones based on the oxidation state of their central heterocycle (Tang et al., 2024) Their structural diversity arises from modifications such as glycosylation, methylation, acylation and polymerization. For example, rutin is a glycosylated flavonoid in figs, while isorhamnetin is a methylated flavonoid in pomegranate. Anthocyanin acylglucosides are acylated flavonoids in black carrots, while proanthocyanidin oligomers are polymerized flavonoids in cranberries. Flavonoid biosynthesis and accumulation in fruit plants are tightly regulated processes. Key transcription factors, including R2R3, bHLH and WD40, are from the regulatory complexes that control these pathways. (Jiang et al., 2023). Environmental factors also affect flavonoid levels, with UV-B irradiation inducing flavonol synthase (FLS) gene expression in strawberries and cold treatment promoting anthocyanin biosynthesis in blood oranges. Light factors, including bagging, can greatly affect anthocyanin and proanthocyanidin biosynthesis in mangoes, where bagging can repress anthocyanins but stimulate proanthocyanidins (Zhu et al., 2023). Flavonoid accumulation shows significant variation among fruit species and developmental stages; these processes are strongly influenced by genotype and environmental conditions. This variability makes flavonoids useful indicators for studying fruit quality, stress adaptation and nutritional enhancement in horticultural crops.

1.1.2 Tannins

Tannins are phenolic polymers that can be categorized into condensed tannins (proanthocyanidins) and hydrolyzable tannins (esters of gallic acid) (Tahara et al., 2024; Molino et al., 2023). Ellagitannins, a subclass of hydrolyzable tannins, are particularly found in high amounts in pomegranates and some Rosaceae fruits such as strawberries and raspberries (Benedetti et al., 2023). Condensed tannins show variability in the degree of polymerization and monomer structure; for example, epicatechin-rich polymers are found in apple peels and seeds, while procyanidin B2 and epigallocatechin gallate (EGCG)-like molecules are found in high amounts in lychee pericarp. Hydrolyzable tannins, such as pomegranate (punicalagins and punicalins), have C-glycosidic bonds with glucose, which gives them extraordinary stability and antioxidant activity. Tannins play an important role in plant defence by providing resistance against pathogens and herbivores through their antimicrobial and anti-digestive properties (Mora et al., 2022; Iqbal et al., 2024). The astringency associated with unripe fruits, such as persimmons, is caused by tannin-protein interactions, in which tannins bind to salivary proteins, producing a "dry" effect. Tannin biosynthesis is regulated by various transcription factors, including members of the MYB gene family, which induce the biosynthesis of condensed tannins in fruits by regulating ANR expression (Wu et al., 2024).

1.1.3 Other Phenolics

This group consists of complex lignins and important acids like gallic and caffeic acid. Lignification provides the physical toughness and stress resistance required for plant organs' structural integrity, making it an essential defensive tactic. (Jan et al., 2021)

It binds between cellulose fibres in secondary walls, forming a hard, strong, and water-resistant matrix, similar to reinforced concrete. The complex, cross-linked structure of lignin makes it resistant to microbial degradation, which helps in carbon sequestration in natural systems like mangroves. Besides gallic and caffeic acids, hydroxycinnamic acid derivatives like chlorogenic acid (dominant in plum and apricot) and neochlorogenic acid (in peach) are known to have antioxidant and antimicrobial properties. The lignin in fruits is tissue-specific; for instance, syringyl (S)-lignin is abundant in mature citrus albedo, while guaiacyl (G)-lignin is predominant in young tomato pedicels. Phenolic acids, together with other phenolics, are biosynthesized via the shikimate/phenylpropanoid pathway or the polyketide acetate/malonate pathway (Kumar et al., 2023). Phenolic compounds are mainly synthesized through the

shikimate/phenylpropanoid pathway or the polyketide acetate/malonate pathway (Kumar et al., 2023). They also play an important role in plant tolerance to abiotic stresses such as drought, salinity, heat, and heavy metal exposure (Nicolas-Espinosa et al., 2023). In addition, melatonin has been reported to enhance the biosynthesis of resveratrol and related phenolic compounds in grape seeds by activating genes such as PAL, 4CL, C4H, and STS (Gao et al., 2024).

1. 2. Terpenoids (Isoprenoids)

Terpenoids represent the most structurally diverse group of specialized plant metabolites, all derived from five-carbon isoprene units. They are isoprenoid derivatives formed mainly through the mevalonate (MVA) pathway, starting from acetate (Kabera et al., 2014). Terpenoid biosynthesis involves two pathways, the cytosolic MVA pathway and the plastidic MEP pathway, which produce the C5 precursors isopentenyl diphosphate (IPP) and dimethylallyl phosphate (Bergman et al., 2019). These compounds are of vital ecological importance for direct defence against herbivores and plant pathogenic microorganisms as phytoalexins, as well as indirect defence through the emission of herbivore-attracting volatiles (Li et al., 2023). The most common monoterpene is limonene, which is found mainly in the flavedo or peel and is responsible for the fruit's distinctive smell. (Kahramanoglu & Usanmaz, 2021).

Pollinators and seed dispersers are known to be drawn to these chemicals due to their strong aroma and volatile nature (Wink et al., 2008). Furthermore, carotenoids are the most common pigments that accumulate at high levels in many horticultural species. Mostly, terpenes play an important ecological role in contributing to yellow, orange and red pigmentation in fruits such as mango, papaya, and orange (Sun Tianhu et al., 2018). Terpene synthases (TPSs) are key enzymes responsible for catalyzing the formation of diverse terpenoid compounds; their expression levels are strictly controlled in space and time for maximum functional benefits in ecology (Cheng et al., 2007). Terpenoids exhibit pharmacological activities including antioxidant, anticancer, anti-inflammatory, antimicrobial and neuroprotective, which have wide-ranging implications for the pharmaceutical, cosmetic, food, and biofuel sectors (Câmara et al., 2024). Progress has been made in the production of specific terpenoids in plants and microorganisms for green technologies and sustainable agriculture (Singh et al., 2024). Terpenoid biosynthesis is strongly regulated by environmental factors, developmental stages and cultivar-specific regulation. Understanding these regulatory mechanisms may support future breeding strategies aimed at improving fruit aroma, flavour and stress tolerance.

1.3. Nitrogen-containing Compound

Nitrogen-containing compounds, including cyanogenic glucoside and glucosinolates, are generally derived from amino acid precursor Q12 (Jan et al., 2021). Based on their structural features and heterocyclic rings, alkaloids are grouped into classes such as isoquinoline, pyrrolidine and purine alkaloids, which include compounds like morphine, nicotine and caffeine. These metabolites serve as an important chemical defence against herbivores and pathogenic organisms. Apart from their ecological importance, nitrogen-containing heterocycles are highly valued in pharmaceutical research because of diverse biological activities, including antiviral, antibacterial, anticancer and anti-inflammatory effects (Kerru et al., 2020). Cyanogenic glycosides constitute another group of nitrogen-containing defence compounds that release hydrogen cyanide (HCN), with amygdalin being a well-known example present in almond, apricot, cherry and peach seeds (Mazid et al., 2011). Finally, glucosinolates and sulfur and nitrogen-containing secondary metabolites are predominantly found in plants belonging to the order Capparales, which includes the Brassicaceae family (Tang et al., 2024). Furthermore, nitrogen heterocyclic macrocycles exhibit interesting supramolecular chemistry useful in catalysis and molecular recognition (Grajewski et al., 2022), while new oxidation processes have been developed for the degradation of hazardous nitrogenous compounds (Bhat et al., 2021).

Separating secondary metabolites into phenolic compounds, terpenes, and nitrogenous compounds can be useful; however, this separation might not reveal the full range of biological functions exhibited by these compounds, which remain incompletely understood. Many metabolites serve multiple purposes and may share some of the same biosynthetic pathways. Furthermore, current studies largely focus on each metabolite group independently, rather than examining how they relate to one another functionally. The major classes of secondary metabolites in fruit crops are illustrated in Figure 1.

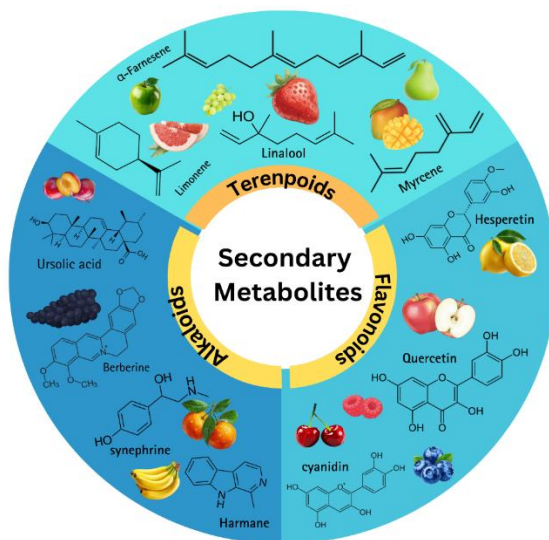


Fig.1 Major Classes of Secondary Metabolites in fruit Crop

2. Metabolic Diversity Across Fruit Crops

2.1 Species-Specific Metabolic Profile

Each species produced a range of species-specific metabolites, despite the 10 fruits sharing 909 common metabolites. (Qi et al., 2021) For example, hundreds of signals specific to individual fruits have been found by large-scale metabolomic analysis. Distinct metabolite profiles, with 706,936,489,104,351,245,440,100,519 and 660 unique metabolic signals, were detected in passion fruit, strawberry, guava, orange, blueberry, mango, apple, grape, mangosteen, and starfruit, respectively, were observed among fruit species. Flavonoid accumulation was highest in mandarin orange, mangosteen, strawberry and starfruit, whereas mango exhibited comparatively lower levels of flavonoids (Qi et al., 2021). In addition to flavonoids, species-specific accumulation also occurs in other secondary metabolites. For instance, certain alkaloids, including harmine and harmaline, are specifically identified in passion fruit pulp. Hydroxycinnamic acid derivatives, including rosmarinic acid, are predominantly found in guava leaves but not in the fruit pulp. Rare triterpenoid saponins, including zizyphus saponins A-C, are specifically found in the fruit pericarp of *Ziziphus jujuba*. Interestingly, starfruit exhibits unusually high concentrations of oxalic acid and caramboxin, which are neuroactive compounds that are present in only trace amounts in other fruits. Interspecific differences in glycosylation patterns, including the abundance of rutinose versus neohesperidose in citrus flavanones, have a direct effect on their bioavailability and antioxidant activity in different species.

2.2 Tissue-Specific Distribution and Biodiversity

The accumulation of metabolites in fruits varies considerably among different tissues. In citrus fruit, juice sacs generally contain lower levels of phenolic compounds than peels and the segment membrane. Citrus peels predominantly contain flavanones, flavone C-glycosides, flavone O-glycosides and polymethoxyflavones (Wang et al., 2017). For example, eriocitrin was found to be a major metabolite of lemon peel, as evidenced by its lower levels in mandarin and, at least in orange peel (Martinidou et al., 2024). Furthermore, the skin's outer layer is particularly rich in aromatic chemicals: Citrus essential oils are composed of diverse volatile bioactive compounds that are mainly stored in exocarp oil glands (Caputo et al., 2020). Other examples of tissue-specific distribution include apples, in which procyanidin B2 and phloridzin are found 5 to 8 times more in the peel than in the flesh, while chlorogenic acid is found in the reverse ratio, 3 times more in the flesh. In grapes, stilbenes such as resveratrol and piceid are found almost entirely in the skins and seeds, with trace amounts in the pulp; this is reflected in the skin-specific expression of stilbene synthase (STS) genes induced by UV-B. In citrus fruits, the membranes of citrus fruit segments contain specific polymethoxyflavones such as nobiletin and tangeretin, which are found in amounts up to 10 times higher than in juice sacs or albedo tissue, due to tissue-specific methylation enzyme activity (OMT isoforms). In mangoes, the mesocarp is found to contain β -carotene in chromoplast-rich cells, while the seed kernel contains mangiferin and benzophenones, which are absent in the edible pulp. Citrus peels are an abundant source of essential oils, flavonoids, carotenoids and phenolic acids (Martinidou et al., 2024; Lu et al., 2021; Wedamulla et al., 2022). Research carried out on different citrus species, including *Citrus reticulata* 'Ponkan', has shown that young leaves roots exhibit the highest antioxidant activity, whereas flavonoids are primarily accumulated in the stem, leaves and peels (Liang et al., 2024). The distribution of flavonoids, limonoids and carboxylic acids in citrus fruits such as aslemon, lime and mandarin highlight the tissue specific nature of metabolites accumulation. (García-Nicolás et al., 2023).

2.3 Chemodiversity and Phytochemical Richness

Fruit crops frequently contain a wide range of substances that support their special ecological and health benefits. Recent phytochemical studies have shown that fruits, seeds, leaves, bark and roots of the genus *Ziziphus* contain diverse bioactive compounds including flavonoids, saponins, triterpenes and alkaloids (Maaiden et al., 2020). Analysis of citrus peels essential oils revealed limonin as the predominant volatile compound across all the species, with concentrations ranging from 88-93% in oranges, 64-93% in mandarins and 55-63% in lemon (Martinidou et al., 2024). Grapes are particularly valued for their abundance of bioactive phenolic compounds, including anthocyanins, flavanols and resveratrol (Liu et al., 2018). However, mango fruit is a rich source of vitamins, carotenoids and phytosterols (Lebaka et al., 2021; Maldonado Celis et al., 2019). Citrus fruits are globally recognized as nutritional health-promoting properties due to their rich content of carbohydrates, vitamins, minerals, dietary fibres, flavonoids, essential oils, carotenoids and limonoids (Lu et al., 2021). Citrus fruit also provides various flavonoids that contribute to fruit colouration, flavour development and stress adaptation (Rao et al., 2019; Zhao et al., 2018). In pomegranates, ellagitannins (punicalagins A/B) account for more than 50% of the total phenolics in the husk and arils, but are nearly absent in flowers and leaves, which contain galloylglucoses and flavone C-glycosides (Zhao et al., 2021).

The differences in metabolite compositions among various fruits occur due to metabolic regulation and adaptation to different environments. However, existing research on fruit metabolomics tends to be conducted on certain fruit types. Some researchers have investigated certain types of metabolites only. Further metabolomic studies need to be performed in order to understand the evolution of metabolites. Secondary metabolites show distinct distribution among different tissues, contributing to fruit colour, aroma, defence, and nutritional quality, is illustrated in Figure 2.

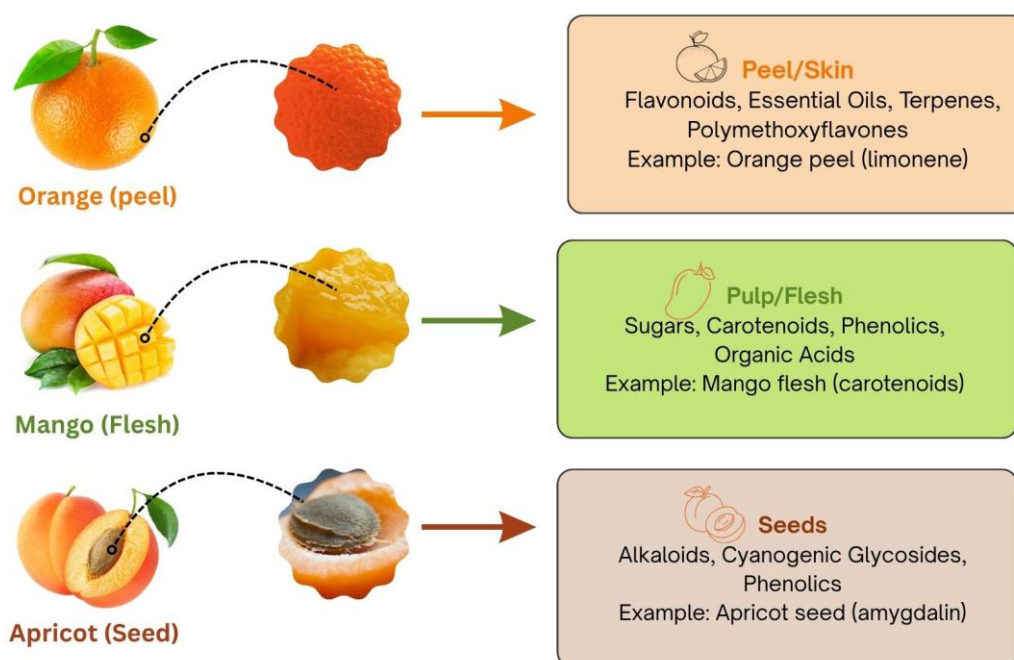


Fig.2- Tissue-specific distribution of secondary metabolites in fruits

3. Functional Role of Secondary Metabolites in Fruit Crops

Fruit crops depend on plant secondary metabolites (SMs) to survive, as they serve as vital mediators in ecological interactions, protect against biological threats, and mitigate physical environmental pressures. In addition to their defensive roles, secondary metabolites significantly contribute to fruit quality by influencing sensory attributes and providing health-promoting benefits to consumers.

3.1 Ecological Interaction and Environmental Communication

Secondary metabolites are essential for plant adaptation to changing environmental conditions; in fruits, they enhance abiotic and biotic stresses while also contributing to traits that attract seed dispersers. (Pott et al., 2019). They are described as multifunctional metabolites that are usually involved in environmental communication and plant defence (Jan et al., 2021; Hartmann et al., 2007). For example, some SMs serve as messengers between plants and their surroundings (Kahramanoglu et al., 2021). Root-derived specialized metabolites (RSMs) play a pivotal role in the rhizosphere, impacting microbial assemblages (Wang et al., 2024). Flavonoids, for instance, are involved in selective interactions between plants and beneficial soil microbiota, thereby facilitating symbiotic interactions (Bag et al., 2022). Fruit microbiota is determined by the secretion of phenylpropanoids and dihydrochalcones, which selectively favour the growth of beneficial endophytes such as *Bacillus* and *Pseudomonas*, leading to improved nutrient uptake and systemic resistance.

3.2 Defence Mechanism Against Biotic Stress

Secondary metabolites (SMs) are a key component of plant innate immunity, facilitating the rapid, localized, and systemic response to biotic stimuli. Upon recognition of the pathogen through the PTI or ETI pathway, plants activate extensive transcriptional changes that stimulate the expression of biosynthetic genes that include PAL, CHS and TPS, leading to the accumulation of antimicrobial secondary metabolites (Al-Khayri et al., 2023; Adhikary et al., 2023). SMs' main purpose is to offer a strong chemical defence against infections and pests. Secondary metabolites serve as barriers against disease invasion, deterrents to herbivores, and oxidative stress mitigators (Jan et al., 2021). These compounds function not only as direct toxins but also as signalling molecules that prime surrounding cells for increased resistance (Wang et al., 2024)

3.3 Antimicrobial and Pathogen Defence

Antimicrobial stress-suppressive metabolites called phytoalexins are typically synthesized in higher concentrations in leaves (Jan et al., 2021; Ahuja et al., 2012). In addition to their antimicrobial activity, certain secondary metabolites promote the formation of structural barriers that restrict pathogen entry and spread (Jan *et al.*, 2021). For instance, plants need phenolic chemicals to protect themselves from pests and parasites (Wuyts et al., 2006). In addition to the toxic effects, some phenylpropanoids (e.g., ferulic acid, sinapic acid) have been observed to enhance cell wall resistance by cross-linking with polysaccharides and lignin precursors (Yang et al., 2023). Flavonoid glycosides such as quercetin-3-O-rhamnoglucoside have been shown to suppress spore germination and appressorium development in *Venturia inaequalis* (Yang et al., 2023).

3.4 Herbivore Deterrence

Terpenes have the power to repel pests due to their strong scent and volatile nature. (Rohmer et al., 1999) In a similar vein, alkaloids like nicotine have been used commercially as pesticides to deter herbivores. (Kahramanoglu *et al.*, 2021 ; Soloway et al., 1976) Condensed tannins (proanthocyanidins), which act as a defensive mechanism by preventing herbivore eating while the fruit is still immature, give many fruits their astringent flavour (Pott et al., 2019) (Manach et al., 2004) Cyanogenic glycosides like amygdalin in apricot kernels and linamarin in cassava are toxic when

released as hydrogen cyanide in response to tissue damage, and are strong feeding deterrents and digestibility reducers for generalist herbivores. Volatile compounds including α -pinene, β -myrcene, and (E) β -caryophyllene are released from injured fruit tissue and function as indirect defence signals by attracting natural enemies of herbivore pests such as parasitoid wasps and predatory mites (Chávez-Arias et al., 2022)

3.5 Protection against abiotic stress

Secondary metabolites provide chemical and physical protection against oxidative stress, mechanical damage, and solar radiation (Pott et al., 2019). Anthocyanins and other phenolic chemicals function as "sunscreens" to shield plant tissues from intense light and UV-B rays. (Jan et al., 2021) (Jaakola et al., 2010). Another defence mechanism used by plants to fend off a variety of pressures is lignification, which gives plant tissues more physical toughness and loading resistance (Jan et al., 2021). Flavonols: Quercetin and Kaempferol glycosides act as enzymatic co-antioxidants in regenerating ascorbate and α -tocopherol during drought and high light stress (Espinosa-Leal et al., 2022). Proline-derived alkaloids (e.g., hygrine in tomato fruit) are accumulated under salinity and heat stress and play a role in osmoprotection (Rehman et al., 2023)

3.6 Organoleptic qualities and attractiveness

The most prevalent pigments that build up in large quantities in the fruit of many horticultural species are called carotenoids; they give numerous fruits, including watermelon, papaya, and mango, their lovely yellow, orange, and red hues (Sun et al., 2018) The red, blue, pink, or purple colors of fruits like strawberries, and cherries are caused by stable coloured compounds called anthocyanins that build up in vacuoles (Mattioli et al., 2020) The most prevalent monoterpene in citrus is limonene, which is largely found in the flavedo/peel and gives the fruit its distinctive smell. Delphinidin-derived compounds impart blue-violet colours in blueberries, while pelargonidin is responsible for bright redness and perceived acidity in strawberries (Saigo et al., 2020). In citrus fruits, limonene combines with esters (such as ethyl butanoate) and aldehydes (such as (E)-2-nonenal) to create variety-specific flavour profiles that are essential for market differentiation (Yu et al., 2023).

3.7 Nutritional and health benefits for consumers

Carotenoids and phenolic compounds possess strong antioxidant activities that may help to reduce the risk of chronic disease (Pott et al., 2019). Fruits high in anthocyanins, such as blueberries, red cabbage, tomatoes, purple sweet potatoes, and eggplants, are prized for their ability to improve health. Dietary intake of fruit-derived SMs is associated with a lower incidence of cardiovascular events, neurodegeneration, and type 2 diabetes, mainly due to activation of the Nrf2/ARE pathway and inhibition of NF- κ B-induced inflammation (Sharma et al., 2023). Ellagitannins present in the arils of pomegranates are converted to urolithins by gut microbiota, which have been shown to have anti-proliferative properties in colon cancer models (Mesa et al., 2023) in particular, the bioavailability and biological efficacy of fruit SMs are strongly influenced by matrix effects, such as the co-consumption of lipids, which increases carotenoid bioavailability, and the fermentation of bound phenolics to produce bioactive short-chain fatty acids in the colon (Pruteanu et al., 2023). Though much is known about the involvement of secondary metabolites in plant protection, stress resistance, and fruit quality improvement, not enough research has been conducted on the regulatory mechanism of these metabolites in a combination of stresses. The majority of studies analyze the effect of one stressor at a time; however, fruits growing in nature experience some stresses at once. The multifunctional role of secondary metabolites in fruit crops is summarized in Figure 3.

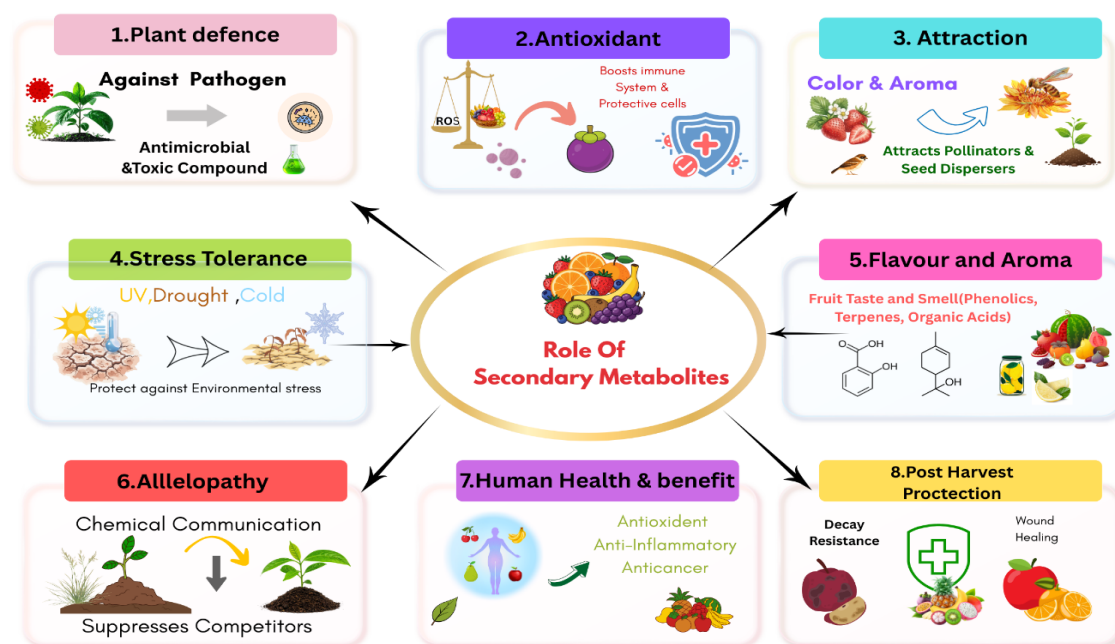


Fig.3 Multifunctional role of secondary metabolites

Table 1 summarizes the major classes of secondary metabolites in fruit crops, their representative compounds, distribution, and biological functions.

Table 1. Secondary metabolites, their classes, functions and associated fruit traits in fruit crops.

Metabolites Class	Key compound	Main Fruit Quality Trait	Example fruit crops	Major function in Fruits	Reference
Flavonoids	Anthocyanins, Flavonols Flavanones	Flesh /skin colour, astringency, antioxidant capacity	Grapes, Strawberry, Citrus, Apple	Pigmentation, antioxidant activity, UV protection, stress tolerance	(Pott et al., 2019)
Phenolic acids	Chlorogenic, caffeic,ferulic acids	Browning potential, bitterness	Apple, pear, peach, cherry	Defence against pathogen,lignificati on Antioxidant defence	(Lin et al., 2023)
Carotenoids	β -carotene, lycopene,lutein	Yellow-red flesh,skin colour,visual quality, nutritional value (Pro-Vitamin A)	Mango, Papaya, Apricot	Light harvesting photoprotection, Precursors of aroma volatiles	(Zhu et al., 2022)
Terpenoids	Monoterpenes Sesquiterpenes Norisopenoids	Aroma, Flavour complexity	Citrus, Mango.Grape, Sweet cherry	Volatile signalling, attraction of pollinators, defence against herbivores	(Yun et al., 2022)
Volatile Esters	Ethyl acetate, hexyl acetate, butyl acetate	Fruity aroma, perceived sweetness flavour	Apple,Strawberry, Banana, Pear	Attraction of seed dispersers,Fruit ripening, signalling	(Pott et al., 2020)

4. Influence of genetic and environmental factors

4.1 Genotype and cultivar variation

A GC-MS-based metabolomic analysis was conducted on strawberry samples from three cultivars cultivated in a soilless system to evaluate variations in primary metabolites including organic acids, amino acids, and sugars (Akhatou et al., 2016). Development and genotype had a significant impact on metabolite profiles. (CARBONE et al., 2009). Even when other environmental conditions remain constant, most plants can have their secondary metabolite composition altered by a single ecological influence (Jan et al., 2021). Secondary metabolism pathways exhibit far more variation at the species, organ, tissue, and cell levels, as well as at various developmental stages, in contrast to the relatively preserved differences of main metabolism events (Wink et al., 2010; Pott et al., 2019). Among the metabolite groups, flavonoids exhibited the greatest variability, with an average coefficient of variation (CV) of 207.91%, while alcohol and saccharide showed the lowest variability, averaging 46.35%. Brigitta and Draper had the greatest levels of anthocyanins (=310.9–311.5) and polyphenols (=511.8–517.3) among cultivars blueberry chemotype and antioxidant qualities are determined by genotype x origin interactions. (Ochmian et al., 2025)

4.2 Climate and agro-ecological conditions

Abiotic environmental stresses, particularly temperature fluctuations, ultraviolet-B (UV-B) radiation, and drought, serve as potent elicitors for the biosynthesis and accumulation of plant secondary metabolites (PSMs). These compounds, including flavonoids, phenylpropanoids, alkaloids, and terpenoids, are not essential for primary growth but are critical for plant survival, defence, and adaptation to adverse conditions. (Espinosa-Leal et al., 2022; Qaderi et al., 2023) The regulation of these metabolic pathways is complex, involving intricate transcriptional networks, signalling cascades, and resource allocation trade-offs that allow plants to mitigate oxidative stress and maintain cellular homeostasis (Gaude & Jalmi, 2025; Jangpangi et al., 2025). Recent research demonstrates that even when other environmental variables are held constant, a single stress factor can significantly reshape the secondary metabolite profile of a plant, highlighting the specificity and sensitivity of these regulatory mechanisms (Mukhopadhyay et al., 2026). Although numerous studies have reported enhanced accumulation of secondary metabolites under environmental stress conditions, the observed responses are not always consistent across fruit species and genotypes. Moderate drought, salinity or UV-B stress often stimulates the production of phenolics and flavonoids by activating antioxidant defence pathways. However, severe or prolonged stress may negatively affect fruit development, yield and overall quality despite increased metabolite accumulation. These contrasting findings suggest that the regulation of secondary metabolism depends on stress

intensity, duration, developmental stage and genetic background. Therefore, a better understanding of genotype-specific responses is required before these traits can be effectively utilized in breeding programs.

4.3 Cultural practices and postharvest handling

The application of phytohormones, including methyl jasmonate (MeJA), salicylic acid (SA) and hexanal, which act as cultural interventions to regulate metabolite levels, is strongly linked to harvesting techniques that improve fruit quality (Ramírez-Castañeda *et al.*, 2025). Moreover, it has been reported that pre-harvest calcium (Ca) treatments in crops such as grapes increase PAL1 expression, resulting in higher flavonol levels at the expense of fruit size and sugar content. (Sánchez-Ballesta *et al.*, 2022). Ripe or senescent fruits frequently undergo metabolic changes after harvest that result in a general loss of qualitative characteristics, such as reduced flavour and the production of "off-aroma" compounds. (Pott *et al.*, 2020). Combining "green engineering" techniques leverages SMs to control postharvest quality. For example, it has been shown that tailored organic formulations with bioactive secondary metabolites, including peptides, phenolic acids, flavonoids, and antifungal lipids, can increase the shelf life of bananas to 45 days while successfully lowering diseases like anthracnose. (Beer *et al.*, 2025).

5. Modern approaches to study metabolic diversity

5.1 Metabolomics: the chemical readout of diversity

Fruit quality, flavour, aroma, and tolerance to biotic and abiotic stressors are all determined by specialized metabolites, which are comprehensively captured chemically by metabolomics. High-throughput technologies enable the identification of metabolites in a variety of fruit species, both targeted and non-targeted. GC-MS, NMR and LC-MS platforms.

In fruits like *Vitis vinifera*, *Garcinia mangostana*, and *Mangifera indica*, LC-MS-based non-targeted metabolomics allows for the comparison of cultivar-specific metabolic markers and the large-scale detection of metabolic characteristics. GC-MS remains the preferred analytical technique for the detection and characterization of volatile secondary metabolites, including terpenoids and esters, which are key contributors to aroma in tropical fruits (Qi *et al.*, 2021). For example, integrated transcriptomic and metabolomic analyses of Hami melon stored at low temperatures revealed that extended cold storage suppresses the biosynthesis of aroma-related compounds (Peng *et al.*, 2024). NMR spectroscopy provides a detailed structural characterization and determination of the absolute configuration of complex secondary metabolites, including flavonoids and other phenolic compounds (Silva Barbosa Correia *et al.*, 2024). This capability is particularly valuable given the extensive structural diversity of metabolites that contribute to fruit quality and human health benefits. (Singh *et al.*, 2023). NMR analysis is superior for highly abundant metabolites, offering direct proportionality to molar concentration for quantification

5.2 Transcriptomics and proteomics

Transcriptomics and proteomics help to identify the genetic regulators and enzymatic steps underlying variation in secondary metabolite accumulation across genotypes, environments, and cultivation practices. Comparative transcriptomic studies have identified R2R3-MYB transcription factors as major regulators of anthocyanin production and other secondary metabolic pathways during fruit development and ripening. For example, PsMYB10 and PsMYB6 have been reported to regulate anthocyanin accumulation in Japanese peach, thereby influencing fruit pigmentation. (Shi *et al.*, 2024). WRKY transcription factors have also been implicated in the regulation of flavonoid biosynthesis and plant response to abiotic stresses in passion fruit. (Ma *et al.*, 2024). Proteomic studies indicate that enzymatic bottlenecks, such as low activity of UDP-glucose: flavonoid 3-O-glucosyltransferase (UFGT), can limit anthocyanin accumulation and explain colour variation in fruit mutants. For example, reduced expression of UDP-glucose: flavonoid 3-O-glucosyltransferase (UFGT) enzyme activity may limit anthocyanin biosynthesis and thus influence the coloration of fruit mutants (Duan *et al.*, 2025) (Duan *et al.*, 2021). The proteome is far more complex than the transcriptome because of post-translational modifications, making proteome analysis difficult but very insightful

5.3 Integration of omics approaches

Integrating multi-omics datasets provides a deeper understanding of the regulatory networks and metabolic control mechanisms underlying secondary metabolite diversity in fruit crops (Gu *et al.*, 2024). This approach is specially value for understanding fruit responses to post-harvest stresses, such as impact injury in apple, which can alter phenylpropanoid pathway (Yang *et al.*, 2023). In *Actinidia melanandra*, multi-omics data analysis has identified the regulatory mechanisms during the soft ripening stages (Gu *et al.*, 2024). Systems-level insights into how protein-level alterations drive metabolic variation across various fruit accessions are provided by integrated proteome-metabolome investigations (Mao *et al.*, 2024). More advanced multi-omics analyses, including metabolome, proteome, transcriptome, DNA methylome, and small RNAome, have been employed to elucidate the metabolic regulatory networks in perennial fruit crops, like the pear (Gu *et al.*, 2024). This integrated strategy enables a better understanding of the intricate relationships between various levels of molecular biology. These methods, in combination, have contributed significantly to the understanding of the complex regulatory networks and metabolic pathways that influence fruit quality and adaptability, which is of immense use in crop improvement and nutritional enhancement (Tohge *et al.*, 2020).

6 Application in breeding and crop improvement

Secondary metabolites are increasingly recognized for their diversity that are not only useful from a scientific perspective but can also be used to bring about practical benefits in terms of enhancing fruit quality, nutritional properties, and stress tolerance. Making use of metabolic information through breeding programs is one such possibility currently being explored.

6.1 Marker-assisted selection

Marker-assisted selection (MAS) is a molecular breeding method that employs molecular markers such as RDMs, GMMs or FMs to facilitate both direct and indirect selection to target genotypes (Salgotra et al., 2020; Collard et al., 2005). MAS's effectiveness is largely dependent on the kind and calibre of molecular markers employed (Gupta et al., 1999). The alleles of the marker must be consistently linked to quantifiable positive or negative effects, and they must be in significant linkage disequilibrium with the alleles of interest in the trait locus. Because FMs are not subject to recombination, they enable accurate and efficient characterisation and screening of germplasm for allelic diversity (Salgotra et al., 2020; Varshney et al., 2005). MAS provides a major advantage over conventional breeding techniques because it allows breeders to choose desirable traits in seedlings, which is more time- and cost-efficient compared to phenotypic selection (Misra et al., 2025). It's particularly valuable for improving traits to evaluate using conventional phenotypic screening, such as those that are expressed late in life, are influenced by multiple genes (quantitative traits) or are affected by environmental factors (Singh et al., 2024). For example, in tomatoes, genome-wide association studies (GWAS) have been used to identify favourable allele combinations of quantitative trait loci (QTL) associated with malic acid, an important contributor to fruit flavour, which illustrates the complexity of metabolic accumulation that MAS can overcome (Gai et al., 2023). MAS has been widely studied and advocated as a means of improving breeding programs in both animal and plant organisms. In fruit crops, MAS is employed for genetic diversity and variety identification, disease diagnosis, hybrid identification, sex identification, and identification of desirable traits (Goswami et al., 2022).

6.2 Biofortification

Biofortification, by boosting the concentration of vital vitamins and minerals through plant breeding, agronomic techniques, or biotechnological instruments, biofortification is a promising and economical way to enhance the nutritional quality of food crops (Zulfiqar et al., 2024). An efficient method of addressing hidden hunger is fruit crop biofortification by gene stacking, which uses a careful balancing act between conventional breeding and metabolic engineering. (Sharma et al., 2023) Developing crop types with naturally increased quantities of nutrients in their edible sections is the main objective of biofortification, making them available to a wider population. (Jha et al., 2025). This is especially important since deficiencies in micronutrients such as iron, zinc, iodine, and vitamin A have been estimated to affect billions of people worldwide, resulting in serious health and development problems (Sandhu et al., 2023). In fruit crops, biofortification may include gene stacking, which ensures a balance between traditional breeding and metabolic engineering (Sabbadini et al., 2021). Although biofortification of staple crops is mainly focused on micronutrients such as iron, zinc, and provitamin A, biofortification of fruit crops is mainly focused on improving health-related secondary metabolites. (De Zanetti et al., 2024). Genetic biofortification is specifically designed to improve the availability of essential nutrients in edible plant parts (Zulfiqar et al., 2024). A comprehensive overview of biofortification in fruits can be presented by categorizing the target nutrient and compounds, the specific fruit crops and the methods employed, along with their observed outcomes. Examples of biofortification approaches for enhancing secondary metabolites in fruit crops are presented in Table 2.

Table2. Targeted enhancement of secondary metabolites in selected fruit crops by biofortification and metabolomics.

Fruit crops	Targeted Secondary Metabolites	Biofortification Method	Notable Outcomes	Reference
Citrus	Flavonoid, Coumarins	Genomic Selection, Metabolic engineering	Increased flavonoid content with antioxidant and anti-cancer properties reduces the risk of citrus	(Liang et al., 2024)
Mulberry	Anthocyanin, Carotenoids, Flavonoids	Polyploidy breeding (diploid vs tetraploid)	Tetraploid cultivars showed higher accumulation of secondary metabolites	(Park et al., 2021)
Apple	Flavonoids (chlorogenic acid, Phloretin derivatives)	Metabolomic profiling for cultivar selection	Cultivar with high antioxidant polyphenols identified	(Commisso et al., 2021)
Pomegranate	Alkaloids, phenolics	Metabolomic profiling	Identification of bioactive compounds in seeds and peel	(Farag et al., 2023)

Table 3 summarizes the major classes of secondary metabolites their regulatory factors, functions in fruit quality and stress responses, and their applications in fruit crop breeding.

Table 3. Relationship between secondary metabolite classes, regulatory mechanisms, fruit quality traits and breeding applications

Metabolite Class	Major Regulatory Factors	Fruit Quality / Stress Function	Breeding Application
Phenolics	MYB transcription factors, PAL pathway	Antioxidant activity, disease resistance	Selection of high-antioxidant cultivars

Flavonoids	MYB-bHLH-WD40 complex, UV regulation	Fruit colour and stress tolerance	Marker-assisted selection
Anthocyanins	UFGT, MYB genes	Pigmentation and antioxidant properties	Nutritional quality improvement
Terpenoids	MVA and MEP pathways	Aroma, flavour and pest resistance	Flavour enhancement breeding
Carotenoids	PSY, LCYB genes	Fruit colour and provitamin A activity	Biofortification programs
Alkaloids	OMT and related enzymes	Defence against pests and pathogens	Development of stress-resilient cultivars

Challenges and Future Prospects

Exploiting the metabolic diversity of fruit crops for improved nutritional quality and stress resilience faces major biological and technological challenges, mainly influenced by the complex regulatory networks regulating secondary metabolite (SM) biosynthesis. One of the major constraints is the balance between plant growth and secondary metabolite production of bioactive compounds such as polyphenols and terpenoids may divert resources away from growth-related processes, resulting in lower yield potential (Sanchez-Ballesta et al., 2022). This physiological trade-off is exacerbated by the high sensitivity of SM pathways to environmental fluctuations; while moderate abiotic stresses like drought or salinity can stimulate the synthesis of beneficial metabolites, severe conditions negatively impact overall fruit development and postharvest stability (Kishor et al., 2023). Another concern is the instability of many secondary metabolites after harvest, as storage conditions and microbial activity can alter their concentration and reduce nutritional quality. (Kim et al., 2024). Although significant advances have been made in metabolomics and functional genomics, understanding of secondary metabolite regulation in fruit crops remains incomplete. Most studies have focused on a limited number of economically important fruit species, while many underutilized fruit crops remain poorly characterized. Furthermore, metabolite accumulation is strongly influenced by environmental conditions, making it difficult to distinguish genetic effects from environmental influences. Variations in sampling methods, analytical platforms and data interpretation also limit direct comparisons among studies. Several important research gaps remain. First, the molecular mechanisms linking secondary metabolite biosynthesis with fruit quality traits are not fully understood. Second, integrated multi-omics studies combining genomics, transcriptomics, proteomics and metabolomics remain limited in many fruit crops. Third, relatively few studies have translated metabolomic discoveries into practical breeding applications. Future research should focus on validating candidate genes, metabolic markers and regulatory networks under field conditions to facilitate their utilization in crop improvement programs.

Despite these obstacles, future prospects are increasingly promising due to the convergence of precision genome editing and systems biology. The integration of CRISPR/Cas technologies with multi-omics data enables the targeted modulation of key enzymes and transcription factors within SM biosynthetic pathways, allowing for the enhancement of specific health-promoting traits without the linkage drag associated with traditional crossing (Biswas et al., 2023; Borah et al., 2024). Future research will likely prioritize elucidating the crosstalk between hormonal signaling networks, such as ethylene and abscisic acid, and secondary metabolism, providing new mechanistic targets for regulating ripening and extending postharvest quality (Kishor et al., 2023). Ultimately, the synergy of precise genetic engineering, advanced metabolomic profiling, and ecological insights will drive the development of next-generation fruit crops that are both nutritionally superior and resilient to climate change (Lv et al., 2024).

CONCLUSION

Metabolic diversity of fruit crops is a remarkable evolutionary feat, where a large array of secondary metabolites, including phenolics, terpenoids, and nitrogen-containing compounds, act as the major interface between the plant and its environment. These substances are not only byproducts of metabolism but are crucial functional molecules that support plant survival through herbivore deterrence, antimicrobial defence, and protection against abiotic stresses such as UV radiation and oxidative damage. These metabolites are the primary factors that determine fruit quality from both a horticulture and consumer standpoint. They contribute distinctive hues (carotenoids and anthocyanins) and nuanced scents (volatiles) that characterize the organoleptic characteristics. These are essential for the marketability and spread of seeds. Additionally, the substantial health benefits of these substances, especially their anti-inflammatory and antioxidant capacities emphasize the fruit crops' nutritional significance in the human diet. However, as this research has shown, the variety and concentration of SMs are extremely dynamic and are controlled by a complex interaction between environmental conditions and genotypic variation. These chemical profiles are further modulated by cultural techniques and postharvest processing, which present the agricultural sector with both opportunities and challenges for future crop improvement strategies. Future advances in metabolomics, integrated multi-omics approaches and genome-editing technologies are expected to significantly enhance our understanding of secondary metabolite regulation in fruit crops. These tools will facilitate the development of nutritionally enriched and stress-resilient cultivars with improved fruit quality and health-promoting properties. A deeper understanding of metabolic pathways and their regulatory networks will support sustainable crop improvement strategies and contribute to the growing demand for functional foods and climate-resilient horticultural production.

DECLARATIONS

Ethical Approval

Not applicable. This review article is based entirely on published literature and does not involve studies on humans or animals.

Consent to Participate

Not applicable.

Consent for Publication

Not applicable.

Competing Interests

The authors declare that they have no competing interests.

Authors' contributions

SRR conceptualized the study and formulated the manuscript. DV edited, reviewed and approved the final manuscript. JA contributed to the development of the ideas and reviewed the manuscript. RJ assisted in summarizing and revising the manuscript. DJ reviewed the final manuscript. All authors read and approved the final manuscript.

Funding

The authors received no specific funding for this work.

AI Declaration: The authors declare that OpenAI was used only for language refinement, grammar correction, and improving the clarity of the manuscript. No artificial intelligence tool was used for data analysis, interpretation of results, or generation of scientific findings. The authors take full responsibility for the content of the manuscript.

Data Availability

No new data were generated or analyzed during this study. Data sharing does not apply to this article because it is based exclusively on published literature.

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