

Review

Organ-Specific Distribution and Functions of Major Secondary Metabolites in Tomato

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Abstract

Tomato is an economically important crop, and its secondary metabolites produced in leaves, fruits, and roots are crucial for environmental stress responses and fruit quality formation. Leaf glandular trichomes mainly synthesize defensive compounds, fruit development involves metabolic transitions, and root exudates act as key signals regulating rhizosphere microbial interactions. However, a comprehensive organ-specific understanding of this metabolic network remains fragmented. This review synthesizes the general theoretical framework of plant secondary metabolism. Using tomato as a model plant, it systematically explores the compositional features, functional differentiation, and regulatory mechanisms of secondary metabolites across leaves, fruits, and roots. We emphasize how metabolic partitioning orchestrates the trade-offs among defense, quality, and symbiosis, and highlight existing knowledge gaps, including the insufficient functional characterization of root metabolites and unclear cross-organ transport mechanisms. Future studies should focus on: (1) functions of root-specific metabolites (e.g., acylsugars); (2) molecular mechanisms of long-distance transport; (3) genetic associations of metabolic reprogramming during domestication; (4) transcriptional regulation of carotenoid cleavage; and (5) domestication selection modules coordinating defense and fruit quality. Integrating spatial metabolomics, single-cell transcriptomics, and gene editing to construct a spatiotemporal regulatory network will provide a theoretical foundation for the coordinated improvement of stress resistance and fruit quality.

Keywords: tomato; organ specificity; secondary metabolites; glandular trichomes; flavor quality; rhizosphere interactions



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1. Introduction

Secondary metabolites are crucial in plant–environment interactions [1]; they not only confer resistance to herbivorous insects or attract pollinators to promote plant reproduction, but also mediate chemical communication between plants [2] and play important regulatory roles in plant growth, development, and stress responses. The realization of these functions is often closely associated with their sites of biosynthesis within the plant.

Tomato belongs to the Solanaceae family and is one of the most widely cultivated vegetables or fruits in the world [3,4]. Secondary metabolites in tomato leaves and roots serve as key signals for perceiving and responding to the environment [5,6]. Tomato fruit is rich in various health-promoting bioactive compounds, such as phytosterols, carotenoids, and flavonoids [7]. Notably, modern cultivated tomato was domesticated from wild tomato [8], and during this process, domestication altered the accumulation patterns

of secondary metabolites in different organs. Given this domestication history, a brief comparison with wild tomato relatives is warranted. Wild tomato species, such as *Solanum pimpinellifolium*, *S. pennellii*, and *S. habrochaites*, are native to western South America, ranging from Ecuador to northern Chile, with several species endemic to the Galápagos Islands [9]. Their fruits are generally small and vary in edibility, with some being locally consumed and others unpalatable or toxic. In contrast to potato (*S. tuberosum*), whose wild relatives are mainly used for tuber traits, wild tomato relatives are primarily exploited for fruit quality and aboveground stress resistance [10]. This domestication-driven metabolic reshaping is exemplified by the reduction of bitter and toxic steroidal glycoalkaloids (SGAs) in fruit to meet human taste preferences [11]; however, this may have come at the expense of the accumulation of defensive compounds in leaves and stems, making cultivated varieties more susceptible to pests and diseases. In addition, breeders have focused on agronomic traits such as shelf life, fruit appearance, and pest and disease resistance, while neglecting the domestication-related loss of key metabolites that contribute to flavor quality [12].

Although considerable progress has been made in characterizing tomato secondary metabolism, existing reviews have largely focused on individual organs, organ-specific themes (most commonly fruit quality or leaf defense), or single biosynthetic pathways. What remains lacking is a systematic cross-organ framework that integrates metabolic specialization across leaves, fruits, and roots and clarifies how shared upstream precursor pools are partitioned among organs to fulfill distinct biological functions. Such an organ-specific, integrative perspective is essential for revealing knowledge gaps that are difficult to detect in single-organ or single-pathway studies.

Therefore, to elucidate the characteristics of metabolic reprogramming in different organs during domestication and their effects on plant adaptability and fruit quality, this review first establishes a theoretical framework for plant secondary metabolism; then, using tomato as a specific case study, it systematically reviews, from an organ perspective, the distribution, functional differentiation, and regulatory mechanisms of secondary metabolites in leaves, fruits, and roots, and analyzes the regulation of metabolic partitioning among organs; finally, on this basis, it identifies knowledge gaps that are difficult to reveal in studies focusing on a single organ or a single pathway and proposes future research directions, aiming to provide a metabolic-level theoretical framework for the coordinated improvement of tomato quality and resistance.

2. Ecological Adaptation and Metabolic Network Basis of Plant Secondary Metabolism

Plant secondary metabolites are key chemical mediators formed during long-term evolution to adapt to complex ecological environments, with functions in defense, reproduction, and communication [13]. Unlike primary metabolites (sugars, amino acids, fatty acids, etc.), which directly participate in growth, development, and energy metabolism, secondary metabolites generally do not participate in basic life-sustaining processes, but play irreplaceable roles in plant–environment interactions. Since plants cannot escape unfavorable environments by movement, secondary metabolism has become an important survival strategy for environmental adaptation. Its ecological functions can be summarized into three aspects: defense, reproduction and dispersal, and communication and symbiosis. In terms of defense, plants synthesize and store or release secondary metabolites with toxic or antimicrobial activities to defend against herbivorous insects, bacteria, fungi, viruses, etc. [14]. In terms of reproduction and dispersal, the color changes and synchronized release of aroma volatiles during fruit ripening constitute dual visual and olfactory signals that attract frugivores to feed and aid seed dispersal [15]. In terms of communication and symbiosis, secondary metabolites act as chemical signals to mediate warning communication

between plants and the recruitment of beneficial rhizosphere microorganisms [16]. These ecological functions indicate that secondary metabolism is not only a physiological strategy for individual plants to adapt to the environment but also mediates chemical dialogues between plants and surrounding organisms. Understanding this ecological adaptation logic is a prerequisite for further analyzing organ-specific metabolic networks in specific crops such as tomato.

The realization of these ecological functions depends on the structural diversity of plant secondary metabolites. Based on biosynthetic precursors, structural features, and functional properties, secondary metabolites in tomato can be broadly classified into terpenoids and their derivatives, fatty acid derivatives, phenylpropanoids and benzenoids, branched-chain amino acid (BCAA) derivatives, acylsugars, and alkaloids (mainly SGAs). The biosynthesis of these compounds originates from three major upstream routes: the shikimate pathway, the methylerythritol phosphate (MEP) and mevalonate (MVA) pathways, and the lipoxygenase (LOX) pathway (Figure 1). On these core skeletons, structural diversity is further enriched through modification reactions such as glycosylation, acylation, methylation, and hydroxylation. In the following sections, the biosynthetic pathways, ecological functions, and molecular regulatory mechanisms of these metabolite classes are comprehensively reviewed.

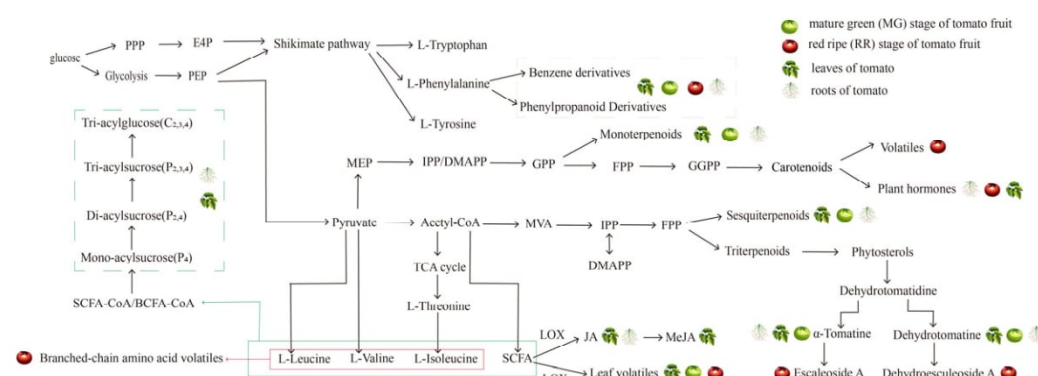


Figure 1. Biosynthetic pathways of plant secondary metabolites. Glucose generates phosphoenolpyruvate (PEP) and erythrose-4-phosphate (E4P) through glycolysis and the pentose phosphate pathway, both of which enter the shikimate pathway and drive the synthesis of benzenoid derivatives and phenylpropanoid compounds. Pyruvate and acetyl-CoA serve as key branching substrates that feed into the methylerythritol phosphate (MEP) and mevalonate (MVA) pathways, respectively, as well as the lipoxygenase (LOX) pathway, and jointly participate in branched-chain amino acid metabolism and acylsucrose biosynthesis. The MEP pathway generates carotenoids, whereas the MVA pathway produces sesquiterpenoids and triterpenoids; phytosterols downstream of triterpenoid metabolism serve as biosynthetic precursors of steroidal glycoalkaloids (SGAs). The LOX pathway is responsible for the generation of jasmonic acid (JA), methyl jasmonate (MeJA), and green leaf volatiles (GLVs); branched-chain amino acids can be converted into branched-chain amino acid-derived volatiles, and the figure also covers the acylsucrose biosynthetic process. Solid arrows represent one or more enzymatic reactions; the leaf, fruit, and root icons labeled next to each metabolite indicate the tissue sites where the metabolite mainly accumulates or is present, and the fruit icon further distinguishes between the mature green and fully ripe stages. Abbreviations: PPP, pentose phosphate pathway; IPP, isopentenyl pyrophosphate; DMAPP, dimethylallyl pyrophosphate; GPP, geranyl pyrophosphate; FPP, farnesyl pyrophosphate; GGPP, geranylgeranyl pyrophosphate; SCFA, straight-chain fatty acids; LOX, lipoxygenase; JA, jasmonic acid; MeJA, methyl jasmonate; BCFA-CoA, branched-chain fatty acyl-CoA.

Phenylpropanoids and benzenoids originate from the shikimate pathway. This pathway uses phosphoenolpyruvate (PEP) from glycolysis and erythrose-4-phosphate (E4P) from the pentose phosphate pathway as substrates, and generates aromatic amino acids

such as L-phenylalanine, L-tyrosine, and L-tryptophan via shikimate and chorismate. Among these, L-phenylalanine is deaminated by phenylalanine ammonia-lyase (PAL) to form *trans*-cinnamic acid [17], which is further modified by hydroxylation and methylation to derive phenolic acids such as caffeic acid and ferulic acid, or condensed via coumaroyl-CoA to enter branch pathways leading to flavonoids and lignans [18]. Salicylic acid can be synthesized independently via the shikimate pathway or generated through the cinnamic acid pathway, and further methylated to form methyl salicylate [19]. In addition, *trans*-cinnamic acid can be converted into benzaldehyde via β -oxidation or non- β -oxidation pathways, and benzaldehyde is a key precursor for benzenoid biosynthesis [20]. These compounds exert biological functions through multiple pathways, including antioxidant defense, photoprotection, disease resistance, and color formation [21]. Their biosynthesis is mainly regulated by the MYB and WRKY transcription factor families, which integrate developmental and environmental signals to precisely control the accumulation of phenolic acids and flavonoids [22].

Terpenoids are synthesized through the methylerythritol phosphate (MEP) pathway and the mevalonate (MVA) pathway, which jointly produce isopentenyl pyrophosphate (IPP) and dimethylallyl pyrophosphate (DMAPP) as two C5 building blocks [23]. Under the catalysis of prenyltransferases, these two building blocks sequentially condense into geranyl pyrophosphate (GPP), farnesyl pyrophosphate (FPP), and geranylgeranyl pyrophosphate (GGPP), serving as direct precursors for monoterpenes, sesquiterpenes/triterpenes, and diterpenes/tetraterpenes, respectively. Monoterpenes and sesquiterpenes are mostly volatile and can directly poison or repel herbivorous insects, or attract natural enemies; carotenoids and their cleavage products contribute to fruit color and aroma [24]. The expression of terpene synthase genes is regulated by multiple transcription factor families such as MYB and ERF. Some MYB transcription factors can directly bind to the promoters of terpene synthase genes and activate their transcription [25]; ERF transcription factors often act as stress-responsive factors, participating in the transcriptional regulation of terpene synthase genes directly or indirectly, and integrating developmental and environmental signals [26]. The differential deployment of this transcriptional regulation across different organs has been clearly evidenced in tomato leaf glandular trichomes [27,28].

Fatty acid derivatives are synthesized via the lipoxygenase (LOX) pathway, which uses C18 unsaturated fatty acids (linoleic acid and linolenic acid) as substrates to generate fatty acid hydroperoxides (HPOs). From these, three metabolic fluxes arise: the allene oxide synthase (AOS) pathway, through a series of reactions, produces jasmonic acid (JA) and volatile methyl jasmonate, which act as defense signaling molecules to regulate various resistance responses; and the hydroperoxide lyase (HPL) pathway produces aldehydes, alcohols, and esters, also known as green leaf volatiles (GLVs); additionally, there is a LOX-dependent, HPL-independent branch (the detailed enzymatic mechanism of which has not yet been fully resolved), producing C5 volatiles (1-penten-3-ol, 1-penten-3-one, etc.), which participate in tomato fruit flavor formation [29]. The JA signaling pathway is regulated by the bHLH transcription factor MYC2, which initiates and amplifies jasmonate-mediated defense responses through a hierarchical transcriptional cascade [30]; whereas the release of GLVs is finely regulated by developmental stage and stress signals.

Branched-chain amino acid (BCAA)-derived volatiles use valine (Val), leucine (Leu), and isoleucine (Ile) as precursors. Their biosynthesis begins with acetolactate synthase, which catalyzes the formation of 2-acetolactate (the precursor of L-valine and L-leucine) and 2-aceto-2-hydroxybutyrate (the precursor of L-isoleucine). Subsequently, L-valine (Val), L-leucine (Leu), and L-isoleucine (Ile) are converted by branched-chain amino acid aminotransferases (BCATs) into their respective α -keto acids, which are further converted into the corresponding aldehyde, alcohol, and ester volatiles [31], representing an impor-

tant source of plant aroma. However, compared with terpenoid and phenylpropanoid pathways, the overall regulatory network of BCAA-derived volatile biosynthesis remains to be further elucidated.

Acylsugar biosynthesis begins with the acylation of the sugar core, and the key enzymes are BAHD superfamily acyltransferases. Four acyltransferases, SIASAT1–SIASAT4, sequentially add acyl chains to specific hydroxyl positions of sucrose, ultimately forming polyacylated acylsugars [32]. This metabolic pathway is positively regulated by the AP2/ERF family transcription factor LEAFLESS, which can directly bind to the promoters of acylsugar biosynthetic genes and activate their expression. The synthesized acylsugars exert insect resistance by disrupting the insect cuticle and through physical adhesion [33].

The SGAs are derived from cholesterol synthesized via the MVA pathway and are converted into α -tomatine through catalysis by the *GAME* gene family, exhibiting broad-spectrum resistance to pests and diseases. When *GAME25* function is lost, the metabolic flux is redirected toward the unsaturated dehydrotomatine branch [34,35]. In potato, the MYB transcription factor encoded by *StMYB113* positively regulates SGA biosynthesis [36]; however, whether an orthologous regulatory mechanism operates in tomato remains to be determined.

Building on the class-specific regulation described above, the final output of secondary metabolism depends on the integration of multiple environmental signals. Environmental factors such as light, temperature, water, and nutrients do not regulate secondary metabolism independently; rather, they are integrated through three routes: altering endogenous hormone levels [37], adjusting carbon–nitrogen balance [38], and affecting precursor metabolic flux [39], ultimately forming a coordinated metabolic output. This enables plants to fulfill the physiological functions of defense, reproduction, and symbiosis in complex environments. This regulatory architecture provides a molecular basis for understanding the organ-specific distribution and functional differentiation of secondary metabolites in plants such as tomato.

3. Organ Specificity in Tomato

Tomato, as a model plant in the Solanaceae family that possesses both significant economic value and a deep foundation in molecular genetics, exhibits a high degree of organ specificity in the types, biosynthetic pathways, and regulatory mechanisms of secondary metabolites in its leaves, fruits, and roots (Table 1). This organ-specific distribution pattern is not random but rather an adaptive strategy formed under the dual drivers of long-term evolution and artificial domestication. From an evolutionary perspective, different organs face distinct ecological selection pressures: leaves, as the aboveground organs in direct contact with the external environment, have long endured multiple stresses such as herbivorous insects, pathogens, and UV radiation, driving them to accumulate defensive compounds such as terpenoids [40]. Fruits, as vehicles for animal-mediated seed dispersal, need to achieve a functional transition from defense to attraction during development: protecting seeds when immature and attracting frugivores through color and aroma when mature [41,42]. Roots, buried in the soil, need to mediate complex interactions with pathogens, beneficial microorganisms, and neighboring plants, and thus contain signaling molecules such as strigolactones [43] (Figure 2). Moreover, artificial domestication has reshaped the metabolic landscape of tomato. Based on the above differentiation, this review analyzes the compositional characteristics, functional realization, and regulatory mechanisms of secondary metabolites in leaves, fruits, and roots, respectively, from the perspective of these three organs.

Table 1. Organ distribution and functions of major secondary metabolites in tomato.

Metabolite Class	Representative Compounds	Leaf	Fruit	Root	Function	Key Genes/Enzymes	References
Terpenoids and their derivatives	Monoterpenes, sesquiterpenes, triterpenes, carotenoids (lycopene, β -carotene), apocarotenoids (β -ionone, 6-methyl-5-hepten-2-one, strigolactones), etc.	Mainly present; monoterpenes predominant, sesquiterpenes secondary	Mainly present; carotenoids and cleavage products	Present; strigolactones, monoterpenes, and sesquiterpenes	Defense, attraction of natural enemies, color, aroma, and mycorrhizal symbiosis	<i>TPS, PSY1, SICCD1, SICCD4, SICCD7/8</i>	[44–46]
Fatty acid derivatives	JA, GLVs [(Z)-3-hexenol, (Z)-3-hexenal, (E)-2-hexenal], methyl ketones, etc.	Present; JA, GLVs, and methyl ketones	Present; GLVs	Present; JA	Direct/indirect defense, signal transduction, grassy aroma, and antifungal activity	<i>LOX, AOS, HPL, TomloxD, TomloxC</i>	[29,47–50]
Phenylpropanoids and benzenoids	Chlorogenic acid, caffeic acid, ferulic acid, methyl salicylate, lignans, 2-phenylethanol, phenylacetaldehyde, guaiacol, eugenol, flavonoids, etc.	Present; chlorogenic acid and flavonoids predominant	Present; 2-phenylethanol, phenylacetaldehyde, guaiacol, eugenol, methyl salicylate, flavonoids, etc.	Present; caffeic acid, lignans, coumarins, flavonoids, etc.	Antioxidant activity, photoprotection, disease resistance, color formation, aroma, and rhizosphere signaling	<i>PAL, C4H, 4CL, AADC2</i>	[44,51–53]
BCAA derivatives	3-/2-Methylbutanal, 3-/2-methylbutanol, 2-isobutylthiazole	Low abundance or not clearly reported.	Mainly present	Low abundance or not clearly reported.	Fruit aroma	<i>AHAS, BCATs</i>	[54,55]
Acylsugars	Acylsucroses, acylglycosylinositols	Mainly present; acylsucroses	Low abundance or not clearly reported.	Present; acylglycosylinositols	Disruption of insect cuticle and physical adhesion to insects	<i>SIASAT1–SIASAT4, SIASAT1-L</i>	[32,56]
Alkaloids (SGAs)	α -Tomatine, esculoside A, dehydrotomatine, dehydroesculoside A	Mainly present; α -tomatine and dehydrotomatine	Mainly α -tomatine at the mature green stage; esculoside A at the fully ripe stage	Present; α -tomatine	Broad-spectrum pest and disease resistance, bitterness/toxicity, and rhizosphere microbial regulation	<i>GAME</i> gene family	[57,58]

Note: The compounds listed in the table are representative major compounds reported in tomato leaves, fruits, and roots, not all metabolites. Variations in cultivar, developmental stage, cultivation conditions, and detection methods may lead to differences in metabolite composition and content. In this table, “Mainly present” indicates metabolites that are relatively abundant or whose functions have been well studied in that organ; “Present” indicates that the compound has been reported; “Not clearly reported” indicates that clear evidence is still lacking in the reviewed literature.

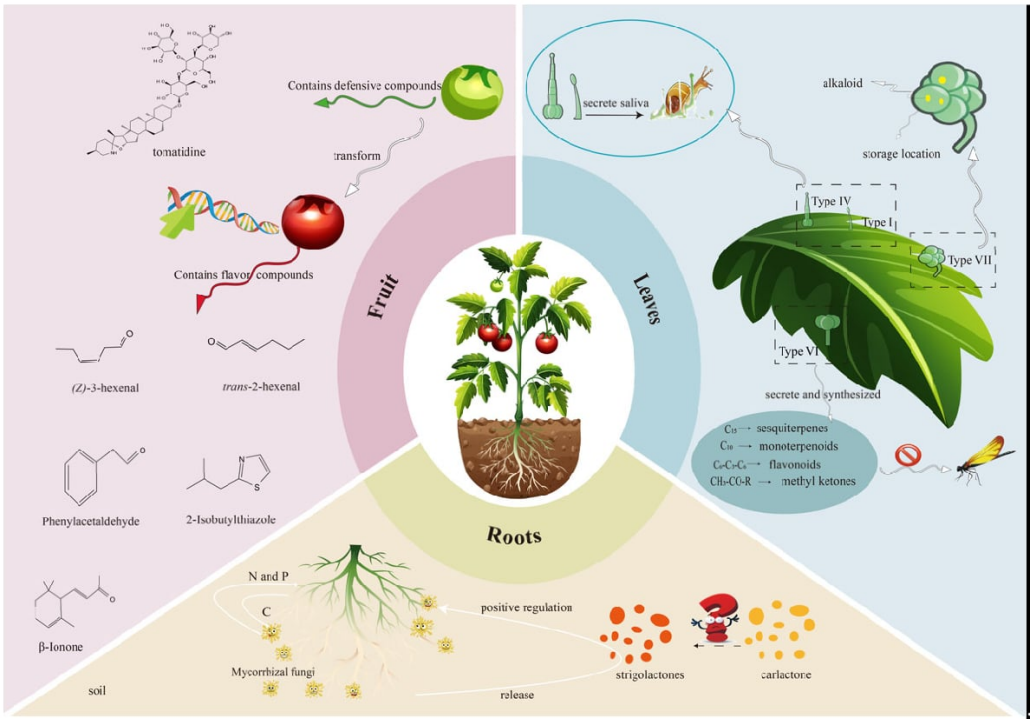


Figure 2. Functional schematic of secondary metabolites in tomato leaves, fruits, and roots. Type I, IV, VI, and VII refer to glandular trichome types. Arrows indicate substance transformation, secretion, transport or regulatory relationships; different background colors distinguish fruit, leaf, and root compartments.

3.1. Multi-Pathway Chemical Defense Mediated by Leaf Glandular Trichomes

3.1.1. Structural Basis and Functions of Trichomes

The most prominent feature of tomato leaves is the highly specialized trichomes, which serve as the interface for plant–environment interactions. Tomato has seven types of trichomes, among which glandular trichomes (types I, IV, VI, and VII) can secrete and store large amounts of secondary metabolites, while non-glandular trichomes (types II, III, and V) mainly prevent insect movement through mechanical barriers or by increasing leaf surface reflectance (Table 2) [59,60]. The core of trichome defense lies in their active perception and signal amplification capacity, and their ecological functions are mainly manifested at two levels: (1) Physical barrier and chemical toxicity: trichome secretions can directly poison or trap pests [61]; (2) Indirect defense: herbivore-induced volatiles can attract natural enemies such as parasitoid wasps [62]. However, domestication has significantly weakened this defense system: type IV trichomes are lost in adult leaves of cultivated tomato, appearing only transiently on cotyledons and juvenile leaves [63]. The metabolic synergy among different trichome types, as well as whether defense traits lost during domestication can be reintroduced through gene editing [64], remains to be explored.

Table 2. Types of glandular trichomes in tomato.

Trichome Type	Characteristics	Major Secondary Metabolites	Distribution	References
Type I	Capitate trichome with a multicellular stalk	Acylsugars	Less abundant in tomato leaves	[65,66]
Type IV	Similar to Type I, but shorter than Type I	Acylsugars	Present only in young leaves of cultivated tomato	[67]

Table 2. Cont.

Trichome Type	Characteristics	Major Secondary Metabolites	Distribution	References
Type VI	Peltate trichome, composed of a multicellular glandular head on a short unicellular stalk	Terpenoids, flavonoids, and methyl ketones	Most abundant type on leaves; widely distributed	[68–70]
Type VII	Peltate trichome with a single stalk cell	Alkaloids (SGAs)	Absent in young leaves of one-month-old wild-type tomato; mainly serves as a storage site and is less involved in biosynthesis.	[65,68,71]

3.1.2. Volatile Defense

Terpenoids are the most abundant and functionally best-characterized class of defensive metabolites in tomato leaves, and are mainly synthesized and stored in type VI glandular trichomes (Table 2). In leaves, monoterpenes (via the MEP pathway) are predominant, followed by sesquiterpenes (via the MVA pathway) [45]. A total of 34 functional terpene synthase (TPS) genes have been identified in the tomato genome, and they exhibit highly specific expression patterns across different organs [72]. Trichome development is positively regulated by the transcription factor encoded by *SISCL3* [73], whereas transcriptional activation of *TPS* genes is directly mediated by MYB transcription factors such as Woolly [74]. These results indicate that leaf terpenoid biosynthesis involves two relatively independent but functionally complementary regulatory layers at the transcriptional level: trichome development, which determines the scale of the biosynthetic site, and *TPS* gene activation, which determines the magnitude of biosynthetic flux.

Fatty acid derivatives are another important class of volatile defensive compounds. The HPL branch of the LOX pathway primarily outputs green leaf volatiles (GLVs), among which (Z)-3-hexenol acts as a plant elicitor to trigger both direct and indirect defense responses against the whitefly *Bemisia tabaci*: on the one hand, it directly interferes with the feeding behavior of *B. tabaci* and inhibits its growth, development, and reproduction; on the other hand, it activates the JA and salicylic acid (SA) signaling pathways, enhancing herbivore-induced volatile release, thereby increasing the attraction of the parasitoid wasp *Encarsia formosa* and improving its parasitism rate on *B. tabaci* [75]. In addition, methyl ketones are another class of fatty acid derivatives that originate from fatty acid degradation intermediates [50]. They are abundant in wild tomato leaves and exhibit strong insecticidal activity, but are present at extremely low levels in cultivated tomato [76], reflecting the loss of LOX pathway-derived defensive metabolism during domestication.

3.1.3. Non-Volatile Defense

In leaves, the phenylpropanoid pathway mainly produces phenolic acids and flavonoids, which primarily perform antioxidant defense and photoprotection functions. Chlorogenic acid accumulates abundantly in tomato leaves and exhibits strong antioxidant activity, scavenging reactive oxygen species (ROS) during stress responses [77]. Flavonoids, in contrast, accumulate in the epidermis and absorb UV radiation [78]. Notably, flavonoids and terpenoids exhibit synergistic interactions in leaves: the flavonoid biosynthesis-deficient *af* mutant shows reduced terpenoid synthesis due to ROS accumulation [79], suggesting that these two major defense metabolic pathways are coupled through a shared redox state, providing important clues for understanding the coordinated integration of multi-pathway defense in leaves. However, whether flavonoid–ROS–terpenoid crosstalk also exists in fruits and roots remains unclear. Fruit-specific CRISPR/Cas9 editing

and virus-induced gene silencing (VIGS) transient silencing systems have been established in tomato [80,81]; single-cell transcriptomics has also been applied to dissect leaf cell subpopulations [82], enabling comparison of the expression differences of flavonoid and terpenoid biosynthetic genes between glandular head cells and stalk cells at single-cell resolution. Using these tools to specifically block the flavonoid pathway can verify whether this synergistic network is specific to leaf glandular trichomes. If this synergistic network also holds true in fruits, it would imply that the accumulation of two important classes of metabolites could be simultaneously regulated through a single target.

Acylsugars are defensive sugar esters unique to glandular trichomes, with sucrose as the sugar core, and are sequentially acylated by four acyltransferases, SIASAT1–SIASAT4, to form polyacylated sucroses. The acyl groups are mainly short- to medium-chain fatty acids, with common acyl chains including acetyl (C2), 2-methylpropanoyl (iC4), and 3-methylbutanoyl (iC5) groups. The chain length can range from C2 to C12, and structural differences in chain length, branching, and saturation determine the physical properties and biological activity of acylsugars [32]. Their insect resistance mechanisms include surface activity that disrupts the insect cuticle (direct toxicity) and high viscosity that adheres and immobilizes small insects (physical barrier) [83]. The transcription factor encoded by *SIWRI3* positively regulates acylsugar accumulation [84].

The SGAs are the main nitrogen-containing defensive secondary metabolites in tomato leaves, exhibiting broad-spectrum resistance to bacteria, fungi, viruses, insects, and herbivorous animals [57]. For example, whiteflies mainly infest the underside of leaves, and the toxicity of these alkaloids can inhibit their feeding, growth, and development [85]. Light induces the expression of genes related to SGA biosynthesis. The light-signaling transcription factors encoded by *HY5* and *PIF3* regulate SGA biosynthesis by directly binding to the G-box elements in the promoters of *GAME1/4/17*, with *HY5* activating transcription and *PIF3* repressing it [86].

3.2. Dynamic Changes in Secondary Metabolites During Fruit Development

The dynamic changes in secondary metabolites during fruit development are essentially a trade-off between seed protection and seed dispersal in plants. Immature fruits must defend against pathogens and herbivores, allowing sufficient time for seeds to develop and mature; after ripening, they must attract animals to feed and thereby achieve seed dispersal.

3.2.1. Dynamic Transition Between Defense and Attraction

SGAs exhibit pronounced dynamic changes in fruits. Immature fruits prioritize defense. At the mature green stage, fruits accumulate large amounts of α -tomatine, which confers bitterness and a certain degree of toxicity, providing resistance to a broad spectrum of pathogens and pests. As fruits enter the ripening stage, α -tomatine is gradually modified and converted into the non-bitter, non-toxic esculoside A, and the defensive properties of the fruit consequently diminish while the taste improves [87]. Beyond the intrinsic regulation of fruit development, domestication has further reduced the accumulation levels of SGAs in ripe fruits. Liu et al. identified the GE1 distal enhancer as a key regulator of SGA metabolism; they found that GE1 has a naturally occurring, more active allelic variant, GE176. During domestication, the less active GE1 allele was preferentially selected and fixed, resulting in significantly lower SGA content in ripe fruits of modern cultivars [88]. This domestication-driven reduction in defensive metabolism in fruits may come at the cost of weakened defense traits in leaves. The GE1 distal enhancer-mediated reduction in fruit SGA levels is a well-documented, experimentally validated example of domestication-driven metabolic rewiring in tomato. By comparison, a CIPK20–MYB28–HAK4 regulatory module conferring salt tolerance has been characterized as a domestication-selected module

in maize [86]. Although this maize finding provides a useful conceptual framework for how domestication may coordinately remodel stress resistance traits at the modular level, it does not constitute direct evidence that an analogous mechanism operates in tomato. Whether comparable domestication-selection modules exist in tomato to coordinately tune leaf defense and fruit quality remains an outstanding question warranting systematic investigation. Future studies could draw on this module research paradigm to reduce fruit bitterness and toxicity while avoiding excessive sacrifice of leaf resistance.

3.2.2. Ripening-Related Volatile Metabolites

Terpenoid metabolism in fruits shifts more toward carotenoid biosynthesis and cleavage, and the resulting apocarotenoids are key compounds determining flavor quality. Carotenoids are cleaved by carotenoid cleavage dioxygenases (CCDs) to generate key flavor compounds such as 6-methyl-5-hepten-2-one and β -ionone [89]. Studies in citrus have shown that the ethylene response factor encoded by *CsERF061* can directly bind to and activate the promoters of multiple carotenoid pathway genes, including *CCD1* and *CCD4*, and heterologous expression of *CsERF061* in tomato fruits significantly promotes carotenoid accumulation [90], suggesting that functionally homologous ERF regulators may exist in tomato. Currently, research on terpenoid regulation in fruits has mainly focused on structural genes such as *PSY1* [91]; in the carotenoid cleavage branch, the functional contributions of *SlCCD1* and *SlCCD4* to fruit aroma quality have been relatively well defined [92,93], but their upstream transcriptional regulators have not yet been fully identified. If key transcription factors regulating *CCD* genes can be identified in tomato, this would provide direct molecular targets for precisely regulating fruit aroma quality through gene editing.

Phenylpropanoid-derived compounds such as 2-phenylethanol, 1-nitro-2-phenylethane, and 2-phenylacetonitrile contribute sweet and floral aromas and are positive flavor factors preferred by consumers, whereas guaiacol, eugenol, and methyl salicylate impart negative perceptions such as “smoky” and “spicy” notes [94]. Notably, elevated methyl salicylate levels reduce the concentrations of key aroma compounds such as amino acid and carotenoid derivatives [95], reflecting a metabolic flux conflict between defense signaling molecules and flavor quality. This contradiction between defense and flavor precisely embodies the partitioning choice faced by the phenylpropanoid pathway in fruits. Branched-chain amino acid (BCAA)-derived volatiles are another important source of tomato fruit aroma, such as 3- and 2-methylbutanal, 3- and 2-methylbutanol, and 2-isobutylthiazole [96]. Feeding experiments have shown that α -keto acids are the direct precursors of branched-chain volatiles, meaning that BCAAs must first be catalyzed by BCATs to generate α -keto acids before entering the volatile synthesis pathway. However, isotope tracing has revealed that the carbon skeletons of BCAAs are mainly directed toward mitochondrial oxidative catabolism to support respiration, with only a small portion used for volatile synthesis [97]. This metabolic configuration reflects an allocation strategy in which energy supply takes priority over quality output during fruit development.

During fruit ripening, the metabolic flux of the LOX pathway is mainly directed toward the HPL branch. The expression of the JA biosynthesis genes *AOS* and *OPR3* is significantly downregulated, and the *SlEIL1* gene weakens defense responses by suppressing JA responses [98]. Meanwhile, the activity of the HPL branch is enhanced, and C6 volatiles such as (*Z*)-3-hexenal, (*E*)-2-hexenal, and (*Z*)-3-hexenol accumulate abundantly, conferring grassy and green aromas to the fruit [99,100]. Knockout of the *Sl-LIP8* gene significantly reduces the content of multiple short-chain fatty acid volatiles in ripe fruits, directly impairing flavor [101], confirming the central role of fatty acid metabolism in flavor formation.

3.2.3. Metabolic Basis of Fruit Coloration

Tomato fruit coloration is one of the core quality traits determining its commercial value and consumer preference, and the chemical basis of coloration is the accumulation of different types and proportions of pigment metabolites in the peel and flesh. Fruit coloration arises from two major pigment metabolic pathways: carotenoids and flavonoids.

Carotenoids are the main contributors to tomato fruit coloration. Red tomatoes have lycopene and β -carotene as their main carotenoids, with lycopene being the most abundant (averaging 26.3–32.5 mg/100 g FW in pink and orange-red fruits); yellow and yellow-green tomatoes have significantly lower lycopene levels (<6.5 mg/100 g FW) and instead accumulate carotenoids such as β -carotene; orange tomatoes have a more complex pigment composition, with higher total carotenoid and β -carotene contents while also accumulating considerable amounts of lycopene [102]. In addition to carotenoids, flavonoids synthesized via the phenylpropanoid pathway also affect fruit coloration. The peel of pink tomatoes is pale in color because flavonoid synthesis is suppressed during fruit ripening, resulting in a lack of naringenin chalcone [103], whereas introduction of the *Aft* gene causes anthocyanin accumulation in the peel, resulting in a purple color [104]. The transcription factor encoded by *SIMYB12* controls flavonoid accumulation in the peel [105], whereas the transcription factor encoded by *SIMYB32* acts as a transcriptional repressor that negatively regulates flavonol accumulation in tomato fruits [106], indicating that the phenylpropanoid pathway in fruits is precisely regulated bidirectionally by activators and repressors.

3.3. Root Metabolite-Mediated Rhizosphere Dialogue

Roots are inhabited by a variety of harmful organisms, including pathogenic fungi, bacteria, nematodes, and root-feeding insect larvae [107,108]. To cope with these stresses, plant roots synthesize and secrete diverse secondary metabolites to enhance their environmental adaptability [109,110]. Notably, the secretion processes of these functionally diverse metabolites in different root regions (such as taproots, lateral roots, root hairs, and root tips) remain unclear [111], and due to the hidden nature of roots and limitations in analytical techniques, research on interactions mediated by belowground volatile signals remains highly challenging [112]. The functions of root exudates can be summarized into two categories: acting as signaling molecules to recruit beneficial microorganisms, and acting as defensive substances against pathogens.

3.3.1. Signaling Molecule-Mediated Establishment of Symbiosis

Strigolactones and flavonoids are key signaling molecules that positively regulate arbuscular mycorrhizal symbiosis. Strigolactones (whose synthesis is initiated by the catalysis of *SlCCD7/8* genes) are carotenoid derivatives that, after being synthesized by roots and released into the soil, act as chemical signals to stimulate the metabolism and branching of arbuscular mycorrhizal fungi, promoting the establishment of symbiosis [113–115]. Their synthesis is positively regulated by the ethylene response factor encoded by *SlERF15* [116]. Absciscic acid (ABA) can synergistically and positively regulate mycorrhizal symbiosis with strigolactones [117], while also acting as a stress signaling molecule to mediate stress responses [118]. Flavonoids can also inhibit root pathogens, stimulate mycorrhizal spore germination and hyphal branching, and are another important class of signaling molecules regulating rhizosphere interactions [119].

3.3.2. Root Defense and Rhizosphere Ecological Regulation

In roots, monoterpenes and sesquiterpenes generally decrease in production under stress, which may be related to a trade-off between constitutive and induced defense [120]. Whether root terpenoid metabolism has a specific trade-off strategy between constitutive

and induced defense still lacks systematic investigation. Fatty acids and their derivatives in root exudates themselves possess antifungal activity [121] and may play a direct role in resisting the invasion of soil-borne pathogens. Exogenous treatment of tomato roots with polyunsaturated fatty acids significantly upregulates the expression of key genes in the JA biosynthetic pathway, such as *9-LOX*, *13-LOX*, and *13-AOS*, indicating the responsiveness of the LOX pathway in roots to pathogens [122]. The phenylpropanoid pathway in roots responds to soil environmental stress. Under salt stress, metabolic changes in caffeic acid, lignans, and coumarins in roots are the most significant [52], and the interaction between the transcription factors encoded by *SIMYB71* and *SIWRKY8* promotes lignin biosynthesis and ROS scavenging [123]. In addition, roots possess a stress-sensing system independent of aboveground parts: after treatment with oligogalacturonides, PAL activity is specifically upregulated only in roots, driving the specific accumulation of compounds such as lignans there [124].

The SGAs in roots have expanded their functions to include rhizosphere ecological regulation. α -Tomatine synthesized in roots can be secreted into the rhizosphere, affecting the composition of soil bacterial communities and enriching beneficial bacteria of the family Sphingomonadaceae [125]. Its constitutive synthesis is redundantly regulated by MYC1 and MYC2, which together with GAME9 coordinately bind to the G-box elements in the promoters of target genes to regulate SGA accumulation [126]. However, the regulatory mechanisms of SGA secretion in roots and the long-term effects of SGA secretion on rhizosphere microbial communities remain to be further explored.

The core structure of acylsugars in roots differs fundamentally from that in leaves: roots use glycosylinositol instead of sucrose as the acylation core, and they also differ in the type, length, and number of acyl chains. From an enzymatic perspective, acylation in leaves is catalyzed by SIASAT1, whereas in roots this function is performed by its homologous enzyme SIASAT1-L [56]. Currently, the biological roles of root acylsugars remain unclear and require further investigation. In future studies, root exudates could be collected and subjected to untargeted metabolomics and 16S rRNA gene amplicon sequencing to establish associations between root exudate composition and rhizosphere bacterial diversity [127], thereby clarifying whether root acylsugars contribute to functions such as recruitment of beneficial rhizosphere bacteria or disease suppression. If this function is confirmed, this would provide new strategies for optimizing the rhizosphere microecology and reducing soil-borne diseases by regulating root metabolites.

3.3.3. Aboveground–Belowground Signal Integration and Plant-to-Plant Chemical Communication

After tomato roots are infected by root-knot nematodes, electrical and ROS signals are transmitted from roots to leaves, inducing JA synthesis; the JA accumulated in leaves is then transported back to roots, forming a root–shoot–root signaling loop that enhances root resistance [128]. After the volatile β -caryophyllene released from tomato leaves is perceived by neighboring tomato plants, it can induce salicylic acid secretion from their roots, resulting in up to 69% similarity in rhizosphere microbial community composition between neighboring and treated plants [129]. Airborne methyl jasmonate (MeJA) also acts as a volatile interplant signal: emission of methyl jasmonate can trigger defensive responses in adjacent plants, representing an early example of aboveground airborne communication in Solanaceae [130]. Such volatile cues may also prime defense signaling networks, sensitizing neighboring plants to mount amplified responses upon subsequent pest or pathogen attack [131]. Therefore, tomato rhizosphere interactions constitute a multi-layered chemical communication network that encompasses direct regulation by root exudates, aboveground–belowground signal integration, and information sharing between plants. However, direct evidence is still lacking regarding whether metabolites such as

alkaloids undergo long-distance transport among leaves, fruits, and roots in response to systemic stress. Although methods such as aphid stylectomy and EDTA-facilitated exudation have been used in phloem transport research, phloem sap metabolomics studies remain very limited overall, and existing data are mainly derived from a few model plants and gramineous crops such as *Arabidopsis*, pea, and maize, due to the difficulty of sampling [132]. Spatial metabolomics has already enabled the visualization of the spatial distribution of more than 30 metabolites in tomato fruits [133]; extending its application to transport channels such as stems and petioles is expected to provide spatial evidence for the long-distance transport of secondary metabolites.

3.4. Regulation of Inter-Organ Metabolic Partitioning

The secondary metabolism of the three organs—leaves, fruits, and roots—of tomato exhibits a clear pattern: a shared upstream precursor pool, with markedly divergent downstream partitioning directions. The formation of this pattern is essentially driven by three underlying factors: the mode of carbon source supply, the developmental status of organelles, and organ-specific transcriptional regulatory networks (Figure 3). Understanding the interplay among these three factors is key to grasping the organ specificity of tomato secondary metabolism.

Carbon availability and allocation patterns are the primary constraints determining secondary metabolic flux in each organ. Tomato leaves are the main photoautotrophic organs; they fix CO₂ through the Calvin cycle to generate triose phosphates, which are then converted via glycolysis and the pentose phosphate pathway into PEP and E4P. PEP-derived pyruvate enters the MEP pathway in plastids, acetyl-CoA enters the MVA pathway in the cytosol, and unsaturated fatty acids enter the LOX pathway (Figure 1). Therefore, secondary metabolic flux in leaves is fundamentally determined by the rate of photosynthetic carbon fixation. Fruits and roots, in contrast, are heterotrophic organs whose carbon supply depends on export from leaves. During early fruit development, chloroplasts are still present and can carry out a certain degree of photosynthesis; however, after chloroplasts differentiate into chromoplasts at maturity, the carbon supply depends on sucrose imported via the phloem [134,135]. Roots have no photosynthetic capacity, and the carbon required for sustained growth and secondary metabolism depends on sucrose transported downward from aboveground parts via the phloem. Thus, from the perspective of carbon allocation, the three organs actually form a source–sink relationship chain: after fixing carbon, leaves allocate it to fruits (quality and reproduction) and roots (signaling and interactions), thereby directing the imported carbon skeletons in each sink organ toward different secondary metabolic end products [136].

The final metabolic fate of carbon skeletons in different organs also depends on the developmental status of organelles. During fruit development, chloroplasts in mature green fruits must simultaneously support photosynthesis and chlorophyll synthesis, and MEP pathway flux is partitioned toward chlorophyll side-chain synthesis; at the ripening stage, chloroplasts differentiate into chromoplasts, chlorophyll is degraded, and MEP pathway flux is globally redirected toward carotenoid biosynthesis, with *PSY1* becoming the rate-limiting node of this branch [137]. In leaves, the plastidial MEP pathway mainly produces monoterpenes, whereas the cytosolic MVA pathway is mainly involved in sesquiterpene and triterpene synthesis; the two pathways operate in parallel in leaves, and IPP can be exchanged between them [138]. Roots are non-photosynthetic organs, and the precursors for their MEP pathway depend on carbon sources imported from aboveground parts, which may result in terpenoid flux in roots being much lower than that in leaves.

Carbon availability and organelle developmental status provide the spatial context for metabolic partitioning. However, the final determination of which branch a carbon

skeleton flows into, and how much end product is synthesized, depends on organ-specific transcriptional regulatory networks. The three organs use the same transcription factor families (MYB, bHLH, ERF, WRKY, etc.) [139], but due to differences in co-regulator composition and other factors, they achieve selective activation of different downstream target genes. This is precisely the fundamental reason for the organ-specific distribution of secondary metabolites.

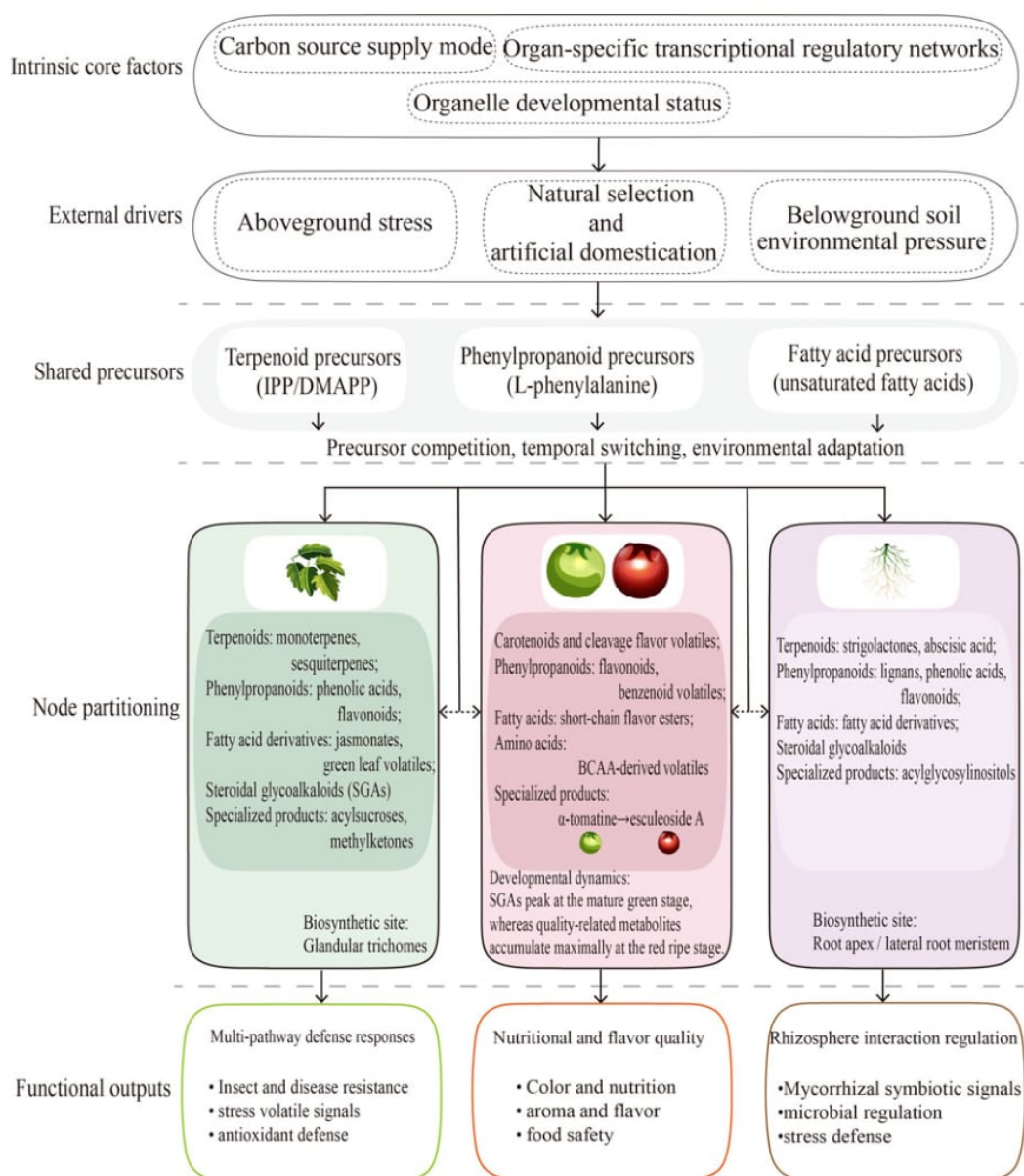


Figure 3. Conceptual framework for metabolic partitioning and functional specialization of secondary metabolism in tomato. Intrinsic core factors (carbon source supply mode, cell developmental status, and organ-specific transcriptional regulatory networks) determine the fundamental landscape of organ-specific partitioning of secondary metabolism. External drivers (aboveground stress, natural selection and artificial domestication, and belowground soil environmental pressure) act as modifying signals that jointly regulate the allocation of shared upstream precursor pools for terpenoids, phenylpropanoids, and fatty acids. Precursor resources undergo organ-specific node partitioning through competition and temporal switching, leading to the synthesis of characteristic secondary metabolites in leaves, fruits, and roots, which respectively fulfill the biological functions of defense responses, nutritional and flavor quality, and rhizosphere interaction regulation. Bidirectional dashed lines represent metabolic signal communication between different organs.

4. Conclusions and Future Perspectives

Tomato secondary metabolism is organized around organ-specific functions: leaves prioritize glandular trichome-mediated chemical defense; fruits undergo a developmental transition from defense to quality and attraction; and roots mediate rhizosphere dialogue and systemic signaling. This partitioning is constrained by carbon supply and organelle developmental status and is executed through organ-specific transcriptional networks, forming a network of shared precursors, node partitioning, and functional conversion.

Figure 4 summarizes the major knowledge gaps and future research directions for organ-specific secondary metabolism in tomato. Future research should prioritize: (i) the biological functions of root-specific metabolites (e.g., acyl sugars) and their roles in rhizosphere microbiome regulation; (ii) inter-organ metabolite transport and aboveground and belowground signal integration; and (iii) the genetic and regulatory basis of domestication-driven trade-offs between defense and quality, including CCD-mediated carotenoid cleavage and aroma regulation. Integrating spatial metabolomics, single-cell transcriptomics, and gene editing to construct a spatiotemporal regulatory network will provide molecular targets for coordinated improvement of stress resistance and fruit quality. Finally, given that climate change is expected to intensify pest and pathogen pressures, developing climate-resilient tomato varieties with an optimized balance between defense and quality is becoming increasingly urgent.

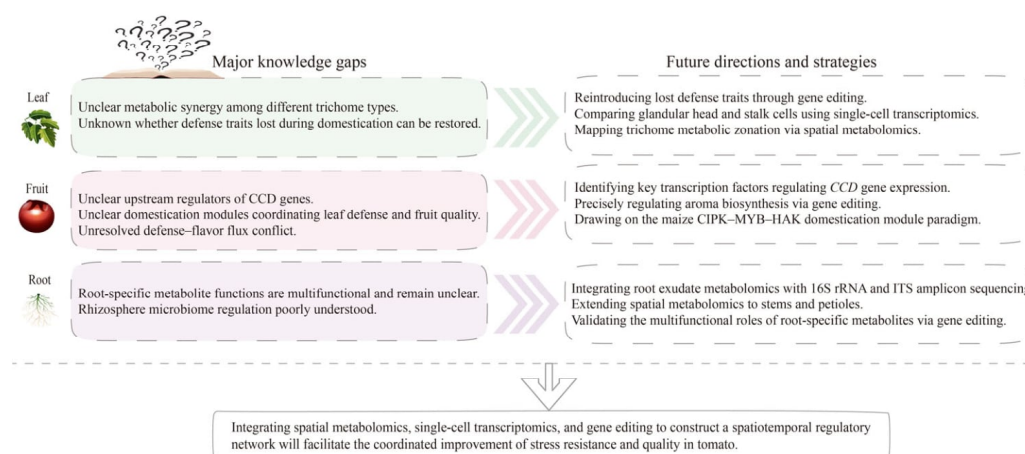


Figure 4. Major knowledge gaps and future research directions for organ-specific secondary metabolism in tomato.

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