Phyton-
International Journal of
Experimental Botany

Tech Science Press

http://doi.org/10.32604/phyton.2026.087213

REVIEW

Glandular Trichomes, Terpenoid Pathways, and Chemotype Interpretation: A Plant-Centered Review of Essential Oil Variability

Radosław Kowalski*

Department of Analysis and Food Quality Assessment, University of Life Sciences in Lublin, Lublin, Poland
*Corresponding Author: Radosław Kowalski. Email: radoslaw.kowalski@up.edu.pl

Received: 12 June 2026; Accepted: 29 July 2026; Published: 28 August 2026

ABSTRACT: Essential oils (EOs) are most commonly characterized by GC–MS profiles and the relative abundance of dominant constituents. This approach is essential for chemical description and quality control, but it does not fully explain why EO composition differs among species, populations, organs, developmental stages, and growth conditions. Here, EO variability is examined from a focused, plant-centered perspective, with emphasis on terpenoid-rich systems in which glandular trichomes or other secretory structures are documented sites of volatile-metabolite biosynthesis, accumulation, or profile variation. The analysis centers on glandular trichomes as metabolic units, MEP/MVA precursor supply, prenyl diphosphate nodes, terpene synthases, and tailoring enzymes, all of which contribute to EO profile formation and chemotype interpretation. The ecological functions of plant volatiles are treated as a regulatory and interpretative background, with a clear distinction between VOC emissions from living plants, the pool of volatile metabolites stored in secretory structures, and EOs obtained by isolation or distillation. Selected model systems, including examples outside classical EO plants, are used as sources of mechanistic evidence on trichomes, terpenoid pathways, and metabolic regulation, rather than as equivalent examples of standard EO raw materials. The review also addresses the limited comparability of EO bioactivity data, which may result from mixture effects, the contribution of minor constituents, matrix-dependent responses, stereochemistry, and changes induced by stress or biotic pressure. The proposed plant-centered workflow integrates taxonomic authentication, herbarium voucher specimens, organ and phenology data, secretory-structure phenotyping, standardized isolation and analytical protocols, and minimal ecological metadata. Chemotypes should therefore be interpreted not solely on the basis of dominant compounds, but as reproducible chemical profiles embedded in the biological, ecological, and methodological context of the plant material.

KEYWORDS: Essential oils; glandular trichomes; chemotypes; terpenoid biosynthesis; volatile organic compounds; secretory structures; botanical metadata; bioactivity

1 Introduction

Essential oils (EOs) are often described in the literature primarily as chemical mixtures: by lists of GC–MS peaks, retention indices, and the percentage contribution of a few dominant compounds [1,2]. This approach is essential for chemical characterization and quality control, but it does not fully explain why EO composition differs among species, populations, organs, developmental stages, and growth conditions [3–6]. Variation in EO profiles results not only from the chemistry of the mixture itself, but also from the taxonomic identity of the plant, the type and maturity of secretory structures, the organization of biosynthetic pathways, genetic background, phenology, and the history of environmental and biotic interactions [3,4,7].

The scope of this review is deliberately focused. It is not intended as a comprehensive monograph of all types of secretory structures or all groups of plants that produce essential oils. The main emphasis is placed on terpenoid-rich systems in which the relationship between glandular trichomes, the organization of biosynthetic pathways, and EO-profile variability has been well documented. Plants of the Lamiaceae family receive particular attention because this group is supported by extensive literature on glandular trichomes, monoterpene biosynthesis, and chemotypes. Selected mechanistic models outside classical EO raw materials are also included. Examples such as *Solanum* and *Artemisia* are used primarily as sources of evidence on trichome regulation, precursor availability, and cell-specific metabolite biosynthesis [8–12]. Related trichome-specific and enzyme-level studies are cited as mechanistic support [13,14], rather than as equivalent examples of standard EO plants in the pharmacopoeial or ISO sense.

Interpreting EO variability requires a distinction among three related but methodologically different levels: VOC emission profiles measured directly from living plants, pools of volatile metabolites stored in secretory structures, and essential oils obtained by isolation or distillation of plant material. These levels may partially overlap in chemical composition, but they are not identical. They depend on compound volatility, tissue localization, storage mechanisms, developmental stage, and the isolation procedure used. For this reason, VOC-emission data are used in this review mainly to interpret ecological regulation, defense induction, and selective pressures; they are not treated as direct equivalents of EO composition unless both levels were analyzed in the same biological material or were explicitly linked experimentally [4,15–17].

Glandular trichomes are among the best-studied examples of the link between anatomy and specialized metabolism. Studies on basil and mint have shown that analysis of glandular material can connect specific oil fractions with particular types of secretory structures and with the activity of terpenoid-pathway enzymes [8–10]. Data on the development of secretory structures and transcriptional regulation further indicate that anatomical and metabolic traits may be coupled through shared regulatory modules [11]. Work on *Mentha* and selected Lamiaceae also shows that variation in the expression of pathway enzymes, terpene synthases, and modifying enzymes can lead to clear shifts in EO profiles and chemotype interpretation [12–14].

The aim of this review is to present a plant-centered interpretative framework for EO variability, with particular emphasis on glandular trichomes, terpenoid pathways, and chemotypes in systems rich in volatile metabolites. The review integrates anatomical, biochemical, ecological, and methodological evidence to indicate when compositional variability may be interpreted as a chemotypic trait, and when it is more appropriately regarded as an effect of organ identity, developmental stage, environmental conditions, biotic induction, or the isolation procedure. This perspective is intended to support more cautious interpretation of GC–MS profiles and more consistent reporting of botanical, technological, and ecological metadata in EO studies [3,4,7,11].

2 Methods/Literature Search Strategy

The review was prepared on the basis of a literature search in the Web of Science Core Collection, Scopus, and PubMed databases, supplemented with queries in Google Scholar (searching and verification of backward citations). The reporting of the literature search and selection strategy was based on recommendations for transparency in reviews and search reporting [18,19]. The searches were conducted between 15 January and 8 May 2026 and covered publications published from 1985 to 2026; the final set of cited references included publications from 1986 to 2026, comprising both classic studies and the most recent reports. Older references were retained when they represented original mechanistic evidence, primary methodological studies, or classic experimental models that have not been replaced by recent

literature. Recent publications were prioritized wherever they provided new experimental data, updated syntheses, or directly relevant examples for glandular trichomes, EO variability, chemotype interpretation, or VOC/EO methodological boundaries. Combinations of keywords were used in titles/abstracts/keywords: essential oil, plant volatiles/VOCs, chemotype, glandular trichomes/secretory structures, terpenoid, terpene synthase (TPS), cytochrome P450, MEP pathway, MVA pathway, monoterpene/sesquiterpene, bioactivity, synergy/antagonism, chiral/enantiomer, as well as the names of selected EO taxa and mechanistic model systems, including *Mentha*, *Thymus*, *Salvia*, *Artemisia*, *Solanum*, and *Origanum*. The selection of these genera was thematic and mechanistic rather than taxonomically representative of all essential-oil-producing plants. *Mentha*, *Thymus*, *Salvia*, and *Origanum* were treated as classical EO-rich systems, particularly within the well-studied family Lamiaceae, and as reference systems for discussing glandular trichomes, monoterpene biosynthesis, chemotypes, and variability in oil composition. *Artemisia* was included as a model of a pharmaceutically important plant in which the relationship between glandular trichomes and specialized metabolism has been well described. *Solanum* was used only as a mechanistic model for type VI trichomes, terpene precursors, and glandular-cell-specific regulation; it was not treated as a standard EO plant or as a pharmacopoeial source of EO. Conclusions drawn from these models are used here to clarify mechanisms, not to generalize directly to all taxa producing essential oils.

The analysis mainly included peer-reviewed original and review articles directly linking botanical/developmental/environmental determinants with the EO or VOC profile (GC–MS profile) and/or biosynthetic mechanisms, as well as publications concerning the methodology and interpretation of bioactivity; publications without taxon authentication or without analytical methods were excluded; papers with an identifiable DOI and complete bibliographic data were preferred. During literature selection and interpretation, studies on EO composition obtained by isolation or distillation were distinguished from studies of VOC emissions measured in living plants. VOC-emission studies were included when they provided information on ecological regulation, defense induction, terpenoid biosynthesis, or the function of secretory structures, but their results were not interpreted as directly equivalent to EO profiles. The quality of the narrative part of the review was verified with reference to tools for assessing the quality of non-systematic reviews (narrative reviews) [20]. This review was designed as a narrative and conceptual synthesis rather than a formal systematic review or meta-analysis; therefore, no quantitative evidence synthesis was performed. In interpreting the literature, four levels of evidence were distinguished: experimental relationships indicating a causal mechanism, correlations observed under field or cultivation conditions, data from well-characterized model systems, and cautious extrapolations between taxa. Model data, for example from *Mentha*, *Solanum*, or *Artemisia*, were used primarily to clarify possible mechanisms of trichome regulation, precursor supply, and terpenoid biosynthesis; they were not treated as automatically generalizable to all EO-producing plants without validation in the taxon concerned.

3 Secretory Structures and Botanical Localization of EO Formation

3.1 Glandular Trichomes as Specialized Metabolic Organs

In many families of aromatic plants, the biosynthesis and accumulation of essential oils are associated with specialized secretory structures: glandular trichomes (GT), secretory ducts, canals and reservoirs, and oil cells located in specific tissues [11,21]. In Lamiaceae, one of the best-studied families in the context of EOs, peltate trichomes are particularly important; in many species they are the main site of biosynthesis and storage of the oil fraction in the subcuticular space [22,23]. Capitate trichomes also occur in this family, but their contribution to the production and accumulation of classical EO is more variable and should not automatically be regarded as equivalent to that of peltate trichomes. Depending on the species and trichome

type, they may secrete smaller amounts of metabolites or other fractions of volatile compounds [11,23–25]. EO composition should therefore be interpreted not only at the level of the whole leaf, but also in relation to the type, maturity, and physiological state of the secretory structures [11,23–25].

However, GT are not merely storage sites. It is increasingly well documented that they constitute specialized metabolic organs in which biosynthesis, modifications, and preparation for accumulation occur in cells with a specific ultrastructural organization and energy metabolism [23,24,26]. In the mint model, glandular secretory cells, despite limited photosynthesis, maintain the high carbon and energy flux required for monoterpene synthesis, while the ATP/NADPH balance is achieved through metabolic solutions typical of specialized production tissues rather than ordinary epidermis [27]. For chemotype interpretation, differences in the energetic and redox capacity of secretory cells may matter even when plants share a similar genetic background. Such differences can shift metabolism toward different end products, including a higher proportion of oxygenated monoterpenes [27,28].

3.1.1 GT Architecture as a Prerequisite for Efficient EO Production and Accumulation

Secretory GT are multicellular structures in which functions are distributed among basal, stalk, and head cells [11,23,29]. In many Lamiaceae, the main structures associated with EO biosynthesis and storage are peltate trichomes, composed of a basal cell, a stalk cell, and several, often eight, secretory head cells [22,23,29]. The head cells constitute the principal site of biosynthesis, while the product accumulates in the subcuticular space or in a chamber within the trichome head [22]. In a classic localization study in mint, it was shown immunocytochemically that enzymes of successive stages of the monoterpene pathway have a strictly defined subcellular localization, for example in plastids or within membrane structures, creating functional “microcompartments” for efficient pathway operation [28]. Such organization limits the loss of volatile intermediates, facilitates substrate transfer between stages, and allows control of the direction of metabolic flux under changing plant requirements for defense and signaling [3,7,28].

Analogous principles can be observed in GT of plants from families other than Lamiaceae, where trichomes function as “factories” of specialized metabolites [21].

In tomato, type VI trichomes have a head composed of several glandular cells and a distinct accumulation space, and variation in this architecture, for example the size of the space and cuticle traits, co-occurs with quantitative and qualitative variation in the secreted terpenes [30,31]. In addition, functional experiments have shown that the transcription factor SlMYC1 simultaneously affects GT development and the terpene profile in glandular cells, demonstrating the coupling of a structural trait and a metabolic trait within a single regulatory module [32].

3.1.2 Compartmentalization of Biosynthesis: From Precursors to the EO Mixture

For chemotype interpretation, GT are not simply sites of terpenoid formation. They also determine the compartment and sequence in which intermediates are produced and modified [33]. In mint and other Lamiaceae, it has been shown that some reactions occur in plastids, including the MEP pathway and the early stages of monoterpene biosynthesis, whereas subsequent modifications, for example oxidations, are strongly associated with membranes and the activity of P450-type enzymes [28]. Such compartmentalization promotes the formation of product sets typical of a given species or chemotype, because it limits the “mixing” of competing reactions and stabilizes flux toward specific end metabolites [3,7,28].

Evidence for GT as metabolic organs is particularly strong in studies based on isolated trichomes or material highly enriched in glandular cells rather than whole leaves [34]. In tomato type VI trichomes, the specific precursor neryl diphosphate (NPP) and NPP-dependent enzymes enable the formation of

monoterpene mixtures characteristic of trichomes, separating them from the metabolic background of the leaf blade [30]. In this model, the GC–MS result should be interpreted primarily as a trichome terpene profile, or as the volatile terpene profile of a defined cell type, rather than as a classical EO profile in the sense of an essential-oil raw material. Enzyme localization and precursor availability within a single cell type can therefore substantially alter the set of terpene products formed [30].

3.1.3 Bioenergetics and Redox Support High Production in GT

Terpenoid synthesis is energetically and reductively costly; therefore, GT efficiency depends to a large extent on how the supply of energy and reducing equivalents is organized [33]. In the study by Johnson et al., it was experimentally shown that in non- or weakly photosynthetic secretory cells of mint, EO biosynthesis is maintained by a specific organization of metabolism that ensures an adequate supply of ATP/NADPH to the terpene pathway [27]. When quantitative differences in EO are interpreted, for example between cultivation variants or stress treatments, three levels should be separated: (i) cellular production capacity, including energy and redox status, (ii) pathway-enzyme expression, and (iii) trichome number and maturity. Integrating these levels helps determine whether EO-profile shifts reflect pathway reprogramming or energetic constraints in secretory cells [27,35,36].

3.1.4 GT as a Regulatory Node: Evidence from Functional Genetics and "Omics"

Functional genetics data provide particularly strong causal evidence linking GT development with specialized metabolism. In the tomato model, this has been demonstrated for the SlMYC1 regulator: silencing or knockout affects the density and morphology of type VI trichomes, as well as the terpene profile in glandular cells, and also involves regulation of pathway genes within the secretory cells themselves [32]. These functional data are complemented by multi-omics/trichome-specific analyses, such as the mapping of transcripts and metabolites within GT, which make it possible to identify multi-level control of carbon flux between the MEP/terpenoid and shikimate/phenylpropanoid pathways in secretory structures [37].

In *Artemisia annua*, the relationship between glandular trichomes and specialized metabolism has been documented mainly for the artemisinin pathway, which is functionally linked with GT [38–40]. The GT-specific WRKY1 factor enhances artemisinin biosynthesis, indicating transcriptional regulation within secretory tissues [39]. The TAR1 regulator, in turn, is required both for trichome development and for the expression of key genes of the artemisinin pathway [40]. Comparative proteomics of trichomes and leaves further showed that GT are enriched in proteins associated with specialized metabolism and secretory physiology [41].

In recent years, high-resolution cellular data have added further value. In *Nepeta tenuifolia*, the use of scRNA-seq made it possible to distinguish cell populations corresponding to peltate GT, identify developmental markers and monoterpene genes enriched in this population, and subsequently reconstruct the differentiation trajectories of glandular cells [42]. In *Artemisia annua*, single-nucleus transcriptomics (snRNA-seq) was applied analogously, showing that the production of key metabolites is strongly "cell-specific" within the gland, which has direct implications for how chemical variability should be interpreted and how sampling for EO analyses should be designed [38].

3.1.5 Methodological Consequences: What Should Be Measured When GT Are the "Biological Unit" of EO

When, in a given taxon, GT have been documented as sites of EO biosynthesis and/or accumulation, or of other volatile terpenoids, sample description and measurements should make it possible to distinguish three sources of variability: (i) the number and type of GT, (ii) GT maturity and the developmental stage of the

organ, and (iii) the metabolic state of the secretory cells. In experimental studies, useful descriptors include GT density per unit area, separately for the adaxial and abaxial surfaces when relevant, the distribution of GT types, head size and accumulation-space parameters, leaf age or phenological phase, and at least one measure of pathway activity, such as TPS/P450 expression in GT-enriched material or selected enzyme activity. Where the aim is to explain qualitative shifts, for example a higher proportion of oxygenated forms, it is also justified to support GC–MS analysis with data on the expression of modifying enzymes and on the redox/energetic conditions of the secretory cells [27].

3.2 Consequences for Reporting and the "Botanical Reliability" of EO Studies

Since the amount and composition of EO are linked to the biology of secretory structures, an oil profile cannot be fully interpreted without basic botanical metadata [43]. In comparative studies, particular attention should be given to taxon authentication, preferably confirmed by a herbarium voucher specimen, the precise definition of the organ or plant part, the developmental stage, and, where possible, features of the secretory structures, such as the type, density, and distribution of GT [44,45]. Not every observed variation in composition, however, should be regarded as a chemotype. For many classical EO raw materials, the organ, harvest phenophase, terminology, and basic quality requirements are already structured by pharmacopoeial, standard-setting, or agronomic practice [46,47]. Metadata recommendations are especially relevant in comparative, field, population-based, and experimental studies, as well as in studies on non-standard material, where such information is often incomplete or not comparable between publications.

The importance of such data is well illustrated by studies in which the traits of secretory structures were analyzed alongside EO composition or yield. Reviews on GT indicate that the number, type, and maturity of secretory structures may substantially affect variability between samples, even within a single species [21,23,24,26]. In *Mentha pulegium*, developmental stage and material origin influenced both trichome micromorphology and the proportions of the main EO constituents, including pulegone, isomenthone, menthone, and piperitenone [35]. In *Lippia origanoides*, simultaneous mapping of GT density and EO composition/yield revealed differences between organs and populations [48], whereas in *Thymus pulegioides*, peltate GT parameters were linked with EO amount, chemotype, and habitat traits [49]. These examples show that some differences attributed to chemotypes may actually result from non-comparable material, such as a different organ, leaf age, flowering stage, or the proportion of tissues particularly rich in GT [35,43,48,49].

The minimum sample description in EO studies should therefore include not an extensive catalogue of all possible variables, but a set of information that makes it possible to assess material comparability: the taxon name and method of identification, a voucher specimen or another confirmation of authentication, the organ/plant part, developmental phase, origin and basic cultivation or habitat conditions, material preparation, and oil-isolation parameters [44,45]. When the aim is to explain mechanisms of variability, this description can be supplemented with simple phenotyping of secretory structures, such as LM/SEM, GT density, distinction between GT types, and, if known, the function of a given trichome type in the taxon studied [21,23,24,26,44]. General metadata standards for plant phenotyping, such as MIAPPE, may also support experimental description and data reuse [50].

Method-related factors are another source of apparent biological variability. Harvest date and harvest phenophase may alter EO yield and composition [51,52]. Drying and the interval between harvest and processing or storage can also affect the oil profile [53,54]. Distillation time may change EO yield, composition, or activity [55–57]. When these steps are not reported, it becomes difficult to determine whether the observed differences arise from plant biology or from material preparation and isolation. The

term “chemotype” should therefore be used with caution: preferably for reproducible chemical profiles obtained from taxonomically, developmentally, and technologically comparable material, rather than for every difference in the percentage contribution of constituents in a single GC–MS profile.

4 Terpenoid Pathways and Biochemical Drivers of EO Diversity

Variability in the EO profile—from quantitative differences to qualitative shifts between chemotypes—is largely a consequence of how the plant distributes and controls carbon flux between isoprenoid pathways and what “enzymatic configuration” it activates in secretory cells [3,7]. In simplified terms, (i) precursor supply (MEP/MVA and their “exchange” between compartments), (ii) the architecture of prenyl diphosphates (GPP/NPP/FPP), and (iii) the set of TPS and “tailoring” enzymes, including P450s, dehydrogenases, and acetyltransferases, jointly form a matrix in which the same species may produce substantially different terpenoid mixtures depending on the organ, developmental stage, and environmental conditions [9,13,16,36].

4.1 Precursor Pathways (MEP/MVA) and TPS/P450 Diversification

Terpenoids—the dominant group of compounds in many oils—are formed mainly from isoprenoid precursors generated in two pathways: the plastidial MEP pathway and the cytosolic MVA pathway. Classically, it is assumed that the MEP pathway primarily supplies monoterpenes (C10), whereas the MVA pathway supplies sesquiterpenes (C15). However, numerous experimental studies show that in living tissues this boundary is “permeable”: depending on the species and cell type, IPP/DMAPP exchange occurs between the plastid and the cytosol, and flux can also be “redirected” to the branch that is limiting at a given moment [58]. This has direct significance for chemotypes: changes in precursor availability may shift not only mono-/sesquiterpene ratios, but also the proportion of oxygenated fractions, indirectly through redox status and P450 activity, as well as the proportions of minor metabolites that modulate the odor and bioactivity of the mixture [59,60].

4.1.1 Evidence for MEP/MVA “Cross-Talk” and Variability in Precursor Supply

Experimental studies using inhibitors, isotope labeling, and flux analyses have shown that the MEP and MVA pathways do not operate entirely independently, and that cells can compensate for disruption of one pathway through changes in the other [58,61,62]. In *Arabidopsis thaliana*, it has been shown that manipulation of precursor availability reveals real metabolite flow between compartments and functional “coupling” of both isoprenoid branches [58]. Comparable evidence from tobacco cell systems shows that blocking one pathway can produce measurable shifts in the other and alter the isoprenoid profile, indicating mechanisms that maintain precursor homeostasis [61].

In the context of epidermal structures, data from tomato trichomes are particularly relevant. In this model, variation in the terpenoid profile was shown to depend not only on differences in TPS expression, but also on regulation of precursor supply and on the preference for plastidial or cytosolic sources, depending on genetic background, that is, wild or cultivated forms [63]. This mechanistic example shows that IPP/DMAPP availability may co-determine the terpene profile in trichomes; applying this conclusion to classical EO chemotypes, however, requires validation in the specific taxon concerned [21,63].

The compartment rule is not absolute. In *Antirrhinum majus* flowers, some volatile sesquiterpenes may be supplied by precursors of the non-mevalonate pathway, indicating that precursor-source mapping can be tissue- and development-specific [62].

4.1.2 Prenyl Diphosphate Nodes: GPP/NPP/FPP Availability in GT

Even with a relatively constant supply of IPP/DMAPP, the "node" stage, involving the synthesis of prenyl diphosphates (GPP/NPP/FPP) and their availability to specific TPS, often determines which final products will be formed [30,63]. In tomato trichomes, it has been shown that monoterpenes in type VI GT may be synthesized from neryl diphosphate (NPP), and not exclusively from classical GPP [30]. A similar role of an alternative precursor has been described in the wild tomato *Solanum habrochaites*, where some sesquiterpenes are formed from Z,Z-farnesyl diphosphate, indicating that the configuration and availability of prenyl diphosphates can substantially reprogram the terpene profile in glandular trichomes [64]. These findings refine chemotype interpretation: chemical differences between populations or cultivars may reflect not only TPS properties, but also regulation of the prenyltransferase node, including which prenyl diphosphate is synthesized and available as a substrate [65,66]. At this point, the tomato examples should be treated as model data on substrate-level control in trichomes, rather than as a direct equivalent of classical EO chemotypes.

Chemotype mechanisms should therefore be separated into at least two levels: (1) changes in precursor supply linked with MEP/MVA activity and metabolite transport, and (2) changes in prenyl diphosphate-node specificity, such as GPP, NPP, or FPP availability. Both mechanisms may generate a similar GC–MS profile, but they reflect different biological and regulatory processes [3,7,30,65,66].

4.1.3 TPS Diversification and Multiproductivity in Chemotype Formation

TPS families have undergone evolutionary expansion, and their functional divergence means that individual enzymes may generate mixtures of products, while small changes in sequence and expression translate into clear quantitative and qualitative differences in the mixture [3,7]. At the cellular level, in systems where EO or volatile terpene profiles are strongly associated with GT, TPS expression may be tissue-specific. The chemical profile then reflects the activity of a relatively narrow set of enzymes that dominate in secretory cells, as shown by classical transcriptomic and functional studies of mint and hop trichomes [10,12]. Consequently, even a subtle shift in expression, for example TPS-A vs. TPS-B, or regulation of a single upstream regulator may produce an effect interpreted as a chemotype change [67,68].

4.1.4 The Final "Composition" of the Volatile Mixture: P450s and Modifying Enzymes as Generators of Qualitative Diversity

While TPS often form the terpene "skeleton", the sensory and biological identity of the oil is determined to a very large extent by "tailoring" reactions: oxidations, hydroxylations, dehydrogenations, and esterifications. Cytochrome P450s play a key role here, as they determine the contribution of oxygenated fractions to the mixture (alcohols, ketones, aldehydes, epoxides), which are often critical for odor and biological activity [69,70].

Mints provide a well-characterized example: regiospecific hydroxylations of limonene are catalyzed by different P450s, and the position of limonene oxidation changes the subsequent course of the pathway and the set of final products [71]. Regiospecific P450 activity can therefore shift an EO profile toward a different oxygenated fraction even when precursor supply and TPS activity are similar [71]. The examples from lavender and mint support a broader interpretation of chemotype formation as a combined effect of TPS specificity, P450-mediated modification, and reaction sequence [14,28,71].

4.2 Chemotype as a Dynamic Chemical Phenotype: Genetic, Developmental, and Environmental Components

Chemotypes are often described as relatively stable chemical variants within a species, identified on the basis of a dominant compound, such as thymol versus carvacrol or menthol versus menthone, or on the basis of a characteristic set of several markers [72–76]. This approach is useful in applied phytochemistry and quality control, but it requires further precision in biological interpretation. In this review, the term "chemical phenotype" refers to the observable profile of volatile metabolites or EO in a given plant material; it is not proposed as an alternative to the classical understanding of phenotype as the outcome of genotype, environment, and G × E interactions. A chemotype may have a strong genetic basis, but its observed profile also depends on the developmental stage of the organ, the type and maturity of secretory structures, growth conditions, and biotic stimuli [5,9,16,36,77]. A review of the genus *Phlomis* emphasizes that EO variability, including variation interpreted as chemotypic, should be considered together with glandular trichomes, organ identity, and growth conditions, since these factors jointly shape both secretory capacity and the configuration of active biosynthetic pathways [77].

4.2.1 Genetic Basis of the Chemotype: From TPS Alleles to the Architecture of Polymorphism

In many aromatic plant systems, there is strong evidence that at least some chemotypes have a clear genetic component, resulting, among other things, from allelic and/or expression differences in TPS families and "tailoring" enzymes, for example P450s, which determine the course of the pathway and the dominant final product (compare the mechanisms discussed in 3.1 and the examples of *Mentha* [13,28,71]; *Origanum* [78]; *Tanacetum* [79]). A well-documented ecological-genetic model is provided by monoterpene chemotypes in *Thymus vulgaris*, where chemical polymorphism is stable at the population level, but at the same time linked to local environmental and biotic pressures [80]. In a study synthesizing field and experimental data, it was shown that chemotypes in *T. vulgaris* can be treated as a component of the plant's ecological strategy, and that their maintenance results from selection and adaptive trade-offs, for example resistance vs. "costs" [73]. An even more "genetically" grounded conclusion comes from a study on monoterpene polymorphism and its hereditary basis in the same species: the authors indicated that differences in oil composition may have the character of a heritable trait, and that the population pattern may reflect genetic structure and selection, rather than only a short-term habitat effect [74].

Accordingly, a chemotype should not be equated with a single GC–MS result, but with a reproducible chemical profile that may be anchored in the genotype, for example in variants of TPS, P450 enzymes, or regulators, yet becomes expressed within a specific developmental and environmental context [81].

4.2.2 Chemotype and Development: "The Same DNA", but a Different Organ, Age, and "Capacity" of Secretory Structures

Even with a strong genetic component, a chemotype may be developmentally modified: the EO profile depends on the maturity of the organ and glands, and on which pathway modules are active at a given moment. Studies on mint show a distinct "leaf-age profile" for monoterpene biosynthesis and the activity of enzymes of the menthol pathway [9], while gland transcriptomics confirms that the composition of the mixture reflects the genes currently active in secretory cells [10,13]. Without strict control of phenology, for example when "leaves" are reported without age or position, a declared chemotype may combine a genetic signal with developmental variation [82]. Such data indicate developmental modulation of the EO profile rather than a distinct chemotype, unless profile reproducibility is confirmed in comparable material and, where possible, across several seasons or populations.

A clearer distinction can therefore be made between:

- a genetically dominant chemotype (a stable pathway direction, for example dominance of one product),
- a developmental/organ chemovariant (a change in proportions within the same "direction" depending on organ age, the contribution of GT-rich tissues, etc.) [83].

4.2.3 Environmental Modulation and G × E Effects

Environmental conditions and G × E interactions may modulate the expression of a chemical profile without necessarily changing its genetic basis. For EOs, growth conditions are especially relevant because they may affect both GT development and density, as well as flux regulation through isoprenoid pathways and the activity of modifying enzymes. In *Mentha*, light intensity can modify trichome density, EO composition, and EO amount [36], while transcriptomic data for *Mentha canadensis* show that light regulates the expression of monoterpene-related genes [16]. As a result, the same cultivar or chemotype may show growth-condition-dependent profile shifts that can mimic chemotypic differences if they are not reported [84,85]. Chemotypic variability may also respond to long-term climate change, as shown for the chemical polymorphism of *T. vulgaris* in the Mediterranean landscape [86].

Moreover, chemotypic variability may be maintained or reinforced by biotic pressure. In an experiment on *T. vulgaris*, selective feeding, using a snail model, was shown to depend on chemotype, which represents an ecological mechanism favoring the maintenance of chemical polymorphism in populations [87,88]: chemotype → ecological interactions → selection → population structure of chemotypes (VOC functions and ecological context [4,17]).

4.2.4 Operational Criteria for Defining and Comparing Chemotypes

Methodologically, "false chemotypes" most often arise when organ and age effects, preparation method, and habitat conditions are mixed in a single comparison. Therefore, a chemotype should be defined operationally as a cluster of repeatable chemical profiles, for example PCA/HCA or mixture modeling, but assigned to material with comparable botanical and technological metadata [75,76,81].

A multiplatform approach supports this operational definition, because the combination of GC–MS compositional profiling with FT-IR/Raman spectroscopy and chemometrics improves chemotype discrimination and result comparability, especially when differences involve sets of covarying constituents rather than a single marker, or when analytical artifacts are possible [72].

GC–MS provides compositional and semi-quantitative information, whereas FT-IR/Raman fingerprints can support rapid chemotype verification and the screening of larger sample sets, particularly in population studies. Together, these levels show that chemotype formation is best interpreted as a regulated sequence of precursor supply, prenyl diphosphate availability, TPS specificity, and subsequent tailoring reactions, modulated by genotype, secretory-cell compartmentation, development, and environment (Fig. 1).

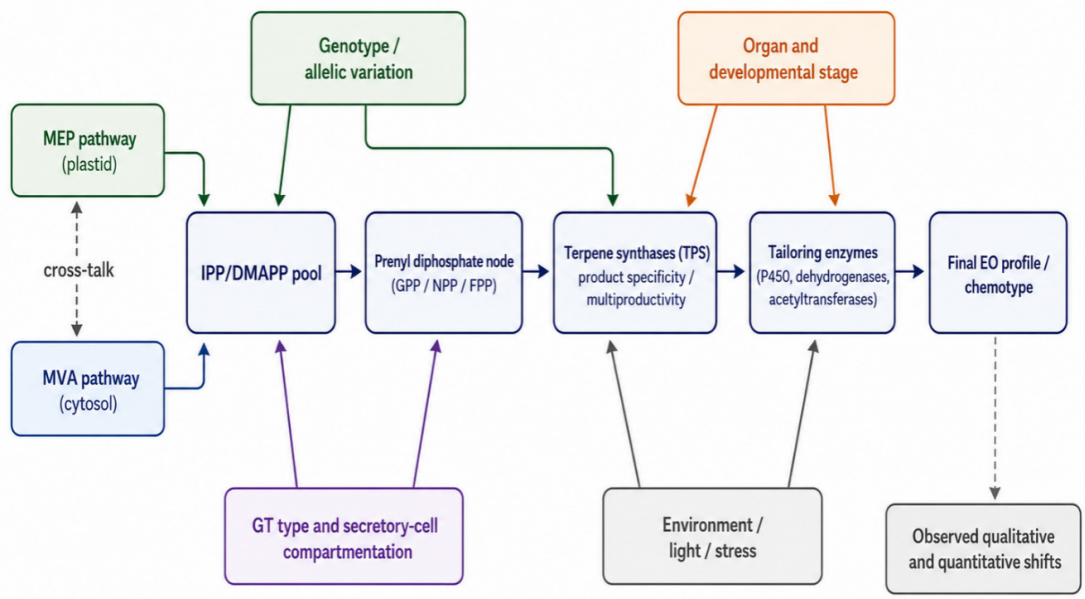

Figure 1: Biosynthetic and regulatory determinants of essential oil chemotypes. The scheme summarizes how MEP/MVA precursor supply, prenyl diphosphate nodes, terpene synthases, and tailoring enzymes jointly shape the final EO profile, with modulation by genotype, GT compartmentation, organ development, and environmental conditions. Abbreviations: MEP, 2-C-methyl-D-erythritol 4-phosphate pathway; MVA, mevalonate pathway; IPP, isopentenyl diphosphate; DMAPP, dimethylallyl diphosphate; GPP, geranyl diphosphate; NPP, neryl diphosphate; FPP, farnesyl diphosphate; TPS, terpene synthases; EO, essential oil; GT, glandular trichomes.

5 Ecological Context of Essential Oil Variability: Lessons and Limits of VOC Studies

The ecology of plant volatile metabolites provides important insight into why the production of terpenoids and other volatile compounds is variable. VOCs are involved in direct and indirect defense, communication with pollinators, plant–plant interactions, and the modulation of relationships within the biocoenosis [3,4,89]. At the same time, these data must be transferred to EO studies with caution. VOC emission from living plants reflects a transient and dynamic physiological state, responses to stimuli, and dispersal conditions, such as wind, temperature, humidity, and the olfactory background [4,90,91]. By contrast, EO obtained by isolation or distillation represents the fraction of compounds recovered from a defined plant material under given technological conditions. A biological link may exist between these levels, especially when the same secretory structures are involved in the biosynthesis and storage of volatile metabolites, but full equivalence should not be assumed. For this reason, the VOC-emission literature is treated in this section as a source of information on ecological functions, induction regulation, and selective pressures that may help interpret EO variability, but it does not replace direct data on oil composition [90,91].

5.1 Direct Defense: Deterrence, Toxicity, and Metabolic Costs

In direct defense, volatile terpenoids and phenylpropanoid compounds may act as:

- repellents and antifeedants, reducing feeding [87,92,93],
- toxic compounds or compounds disrupting herbivore physiology [87,92–94],
- inhibitors of pathogen development, with antifungal/antibacterial activity—often through mixture synergy [92,95,96].

Different EO mixture patterns may have different ecological consequences, for example a predominance of monoterpene phenols versus a higher contribution of the oxygenated fraction [97]. This creates a classic scenario of trade-offs: greater defensive effectiveness may entail metabolic costs or costs in mutualistic relationships, for example potential "disruption" of the signal to pollinators [90,98,99].

5.2 Indirect Defense and Tri-Trophic Recruitment of Herbivore Enemies

The strongest evidence that plant volatile profiles are ecologically inducible comes from the literature on indirect defense: after attack, the plant emits a mixture that acts as information for predators and parasitoids attacking herbivores [4,100–102]. Plants attacked by a herbivore may selectively attract parasitoids through the emission of specific odor signals [100,101,103]. For EO interpretation, the methodological consequence is clear: when plant material originates from populations exposed to different levels of biotic pressure, some apparent "chemotypic" differences may reflect induction or defense priming rather than stable chemical polymorphism [4,100,104,105]. VOC-emission data therefore indicate the possibility of induced regulation of volatile metabolism, but only parallel EO measurement, or analysis of the stored metabolite pool, can show whether this signal is reflected in the oil obtained from biomass. Green leaf volatiles (GLVs) illustrate this point [91,104]: rapid changes in GLV-isomer configuration can create tri-trophic effects by making herbivores more detectable to their enemies, showing that mixture dynamics and timing are biologically relevant [106–109].

5.3 Pollinators and the Balance between Defense and Attractiveness

VOCs also perform functions in mutualistic relationships: odor signals influence flower choice, pollination efficiency, and pollinator fidelity [98,110,111]. At the same time, herbivore pressure may modify floral scent emission and consequently change plant attractiveness to pollinators, providing an empirical example of a potential trade-off between defense and signaling function [99,112–114]. Defensive and communicative functions often operate within the same chemical space [115,116]. A chemotype associated with greater resistance to a particular herbivore may therefore also affect floral scent and pollinator attraction, and the reverse may also apply [98,99,110]. In such systems, chemical polymorphism may be maintained by multiple selective pressures rather than by a single ecological factor [116].

5.4 Plant–Plant Interactions and the Chemical Context of the Neighborhood

In addition to plant–herbivore and plant–pathogen relationships, increasing importance is being attributed to plant–plant interactions, in which volatile metabolites function as signals modulating the behavior and physiology of organisms in the surroundings [117,118]. VOCs may act as information about stress, for example herbivory, infection, or drought; initiate or strengthen defense responses in neighboring plants (so-called priming); and indirectly influence the subsequent course of biotic interactions in the community [4,118–120]. The effectiveness of such signals, and their perception by neighboring plants, depends on dispersal conditions, including microclimate, turbulence, and olfactory background, as well as on the physiological state and interaction history of the receiver [118,119,121].

Chemotype, stored volatile pools, and VOC-emission profiles should therefore be treated as related but distinct components of a plant chemical phenotype. The same set of compounds may perform different functions depending on neighborhood context, and part of the variability observed between sites or cultivation variants may reflect differences in the surrounding chemical context and in the dynamics of plant–plant signals [117,119,120,122].

5.5 Ecological Effects and Bioactivity Differences across Studies

In selected systems, ecological interactions may affect not only VOC emission but also the stored pool of volatile metabolites. This should be verified by direct oil measurement or by analysis of the same plant material [123,124]. In an experimental study, it was shown that variation in ecological interactions, for example pollination regime and simulated herbivory, led to changes in the EO profile and to modification of the measured bioactivity [17]. This observation may explain why some discrepancies in EO bioactivity reported in the literature reflect differences in the plants' biotic history, and often also in microclimate, water availability, and light conditions before harvest [123,124].

5.6 Biotic Metadata and Ecological Reliability in EO Studies

In comparative studies, the interaction history of the plant should be treated as a minimal contextual variable. Many functions of volatile metabolites become evident only after induction, for example following herbivory, infection, or alarm signaling. If biotic pressure is not reported, induced or primed profiles may be misclassified as chemotypes, while variability in bioactivity may be mistaken for poor methodological reproducibility [17,125,126].

A concise biotic record is usually sufficient: visible herbivore damage, disease symptoms, basal versus induced state, stimulus type and time after induction, and the broad biotic setting of the material, such as monoculture, mixed cultivation, or natural population. Sampling should avoid pooling plants with markedly different damage or disease histories, and induction experiments should define the interval between stimulus and harvest. Such documentation remains modest in scope, but it helps protect chemical interpretation when VOC-emission data are used to support conclusions about oil variability [4,117,118,127,128].

6 From Botanical Determinants to Application Effects: Sources of Variability in EO Bioactivity

In application-oriented studies, EOs are often assessed mainly through bioactivity assays, especially in antimicrobial and antioxidant contexts [92,129,130], phytotoxicity [131], and nutraceutical applications [132,133]. The comparability of these results is limited, however, when the chemical profile is not linked with the botanical origin of the material, sample preparation conditions, and the test model [4,17,27,129,134]. Variability in EO "activity" can be reduced to three main levels: (i) mixture effects, including synergy, antagonism, and the contribution of minor constituents, (ii) the influence of the test matrix, which changes the actual availability of active compounds, and (iii) stereochemistry, which is usually not captured by routine GC–MS profiling [92,134–137].

6.1 Mixture Effects and Matrix Dependence

EO activity should not be attributed solely to dominant compounds such as thymol, carvacrol, or menthol, because the mixture may act differently from the sum of the effects of its individual constituents [138–140]. In many biological systems, the final effect depends on the proportions of components, the presence of minor fractions, and mixture interactions [92,95,96,131,140]. Interactions with membranes, enzymes, or other biological targets are also important [141–143]. Compounds that show strong activity in isolation may be enhanced or weakened in the EO by other constituents, including oxygenated monoterpenes, sesquiterpenes, and phenylpropanoids [96,131,139,143].

A second source of variability is the test matrix. In antimicrobial and food-related studies, the presence of fats, proteins, or polysaccharides may reduce the bioavailability of lipophilic fractions and alter the actual exposure of microorganisms to active EO components [95,129,134,142]. Differences between bioassay

results therefore do not necessarily indicate analytical errors. They may reflect differences in the test environment, incubation conditions, or the way activity is operationally defined [72,95,130,134,142].

Minor constituents and oxygenated fractions may be more sensitive than dominant compounds to organ identity, developmental stage, the state of secretory structures, and biotic pressure [4,17,27,30]. As a result, samples with a similar proportion of the main marker may differ in bioactivity if they differ in the profile of co-occurring minor constituents or in the degree of oxidation of the terpene fraction [27,28,139].

6.2 Phytotoxicity and Oxygenated Fractions

EO phytotoxicity clearly illustrates the relationship between mixture structure and biological effect [144,145]. The review by Abd-ElGawad et al. [131] indicates that oxygenated monoterpenes and other oxygenated compounds may contribute substantially to phytotoxic effects, and that structure–activity relationships are particularly evident in this area [131,144,146]. Here, the relevant question is not only which groups of compounds are active, but also why their proportion increases in a given material. Possible causes include GT maturity and metabolic state, the activity of tailoring enzymes, especially P450s, and the effect of stress or defense induction on the flow of metabolites toward oxidized products [16,17,60,69,71]. Phytotoxicity is therefore an example in which SAR relationships can be linked with organ biology, pathway regulation, and stress history [4,9,131,145,147].

6.3 Stereochemistry as Hidden Variability

Stereochemistry is a separate source of variability that may remain invisible in conventional GC–MS without chiral separation [148]. Enantiomers of the same compound may differ in their interactions with receptors, enzymes, or membranes, as well as in sensory properties [92,135,136,148,149]. A similar percentage of a given monoterpene in two samples therefore does not always mean biological or sensory equivalence if the enantiomeric ratio differs [92,135,137,148,150].

Chiral analysis does not need to be a standard component of every EO study, but it is justified when differences in bioactivity or aroma are greater than would be expected from the proportions of dominant compounds [92,135,137,148,150]. This applies especially to comparisons of populations, organs, growth conditions, or materials with similar GC–MS profiles but different biological effects [72,92,135,148,150].

6.4 Application-Oriented Studies and Botanical Standardization

Reviews on nutraceuticals and supplements show the broad potential of EOs, but they also point to the need for control of safety, formulation, and reproducibility of effect [132,133]. For the biological effect to be predictable, application data must be linked with raw-material standardization: taxon, organ, phenology, origin, material preparation conditions, and isolation parameters [27,56,132,151,152]. Without this information, it is difficult to determine whether the observed variability in activity results from mixture properties, the test matrix, stereochemistry, or biological variability of the plant material.

Application-oriented data therefore remain directly connected with botanical standardization. If the developmental history of the organ, the state of secretory structures, or biotic pressure affects mixture composition, it may also indirectly affect the measured bioactivity [17,125,126].

7 Comparative Case Studies: Botanical Determinants and Chemotype Interpretation

Selected examples are compared in Table 1 to show the main types of botanical and technological determinants affecting EO profiles. The set is not intended as a comprehensive taxonomic review. It mainly includes classical or well-justified EO systems in which oil composition can be linked with raw-material

origin, organ identity, phenology, secretory structures, habitat, or cultivation conditions. The mechanistic models discussed in Sections 3 and 4 were not included in the table as classical EO case studies. *Cannabis sativa* was retained only as a terpene-rich industrial material with published data on inflorescence EO yield and composition; it is not presented here as a classical pharmacopoeial EO species.

Table 1: Comparative case studies linking botanical determinants with EO profiles and chemotype interpretation.

Plant System	Main Determinant	Observed Effect on EO Profile	Interpretative Value
Salvia officinalis	Source and provenance of raw material	EO profiles differed among pharmaceutical products, food products, and cultivated raw material [153–156].	Source should be treated as a primary metadata variable; without provenance data, differences may reflect batch selection, blending, or processing rather than biological variation [153–157].
Mentha pulegium	Phenology, organ development, and wild vs. cultivated origin	Developmental stage and origin affected trichome micromorphology and the proportions of major EO constituents, including pulegone, isomenthone, menthone, and piperitenone [35,158–160].	Without control of organ age and developmental stage, a developmental chemovariant may be mistaken for a chemotype.
Thymus pulegioides	Peltate GT parameters and habitat	Peltate GT traits, EO amount, chemotype distribution, and habitat characteristics were interrelated [49,85,161,162].	Chemotype interpretation should include GT phenotyping and habitat data, not only GC–MS profiles.
Lippia origanoides	Organ identity and GT density	Leaves and inflorescences differed in GT density and EO composition [48,163,164].	Different organs of the same plant may represent different EO mixtures because of distinct epidermal and secretory architecture.
Cannabis sativa	Reproductive structures, micromorphology, and cultivation context	Infructescences/inflorescences showed organ- and cultivation-related differences in terpene profile, EO yield, and potential industrial value [165–167]. Glandular-trichome development and metabolite accumulation in reproductive structures have also been documented [168–170].	In terpene-rich industrial material, organ, year, location, and cultivation metadata are necessary for raw-material standardization.
Origanum vulgare	Subspecies/cultivar, cultivation practice, harvest date, and sample definition	EO profiles may be linked to genetic material [78,171,172], but are also affected by cultivation, harvest timing, and the contribution of bracts or inflorescence tissues [173–175].	Chemotype classification requires standardized botanical and technological metadata.

The comparison presented in Table 1 shows that similar shifts in EO composition may arise from different biological or technological causes. In some cases, raw-material origin is decisive; in others, the main factors are organ identity, phenology, GT parameters, habitat, or cultivation practice. Chemotype

interpretation therefore requires comparable material and control of the main sources of organ-related, developmental, environmental, and technological variability.

8 Proposed Plant-Centered Workflow, Conclusions, and Perspectives

The main proposal emerging from this synthesis is a plant-centered workflow (Fig. 2) that brings together five types of information: botanical authentication, phenotyping of secretory structures, controlled chemical analysis, chemometric or multi-platform validation, and basic ecological metadata. Such integration is intended to reduce the risk of attributing EO-profile variability solely to chemotype when it may instead arise from organ identity, phenology, GT status, the isolation procedure, or the history of stress and biotic interactions [4,17,72].

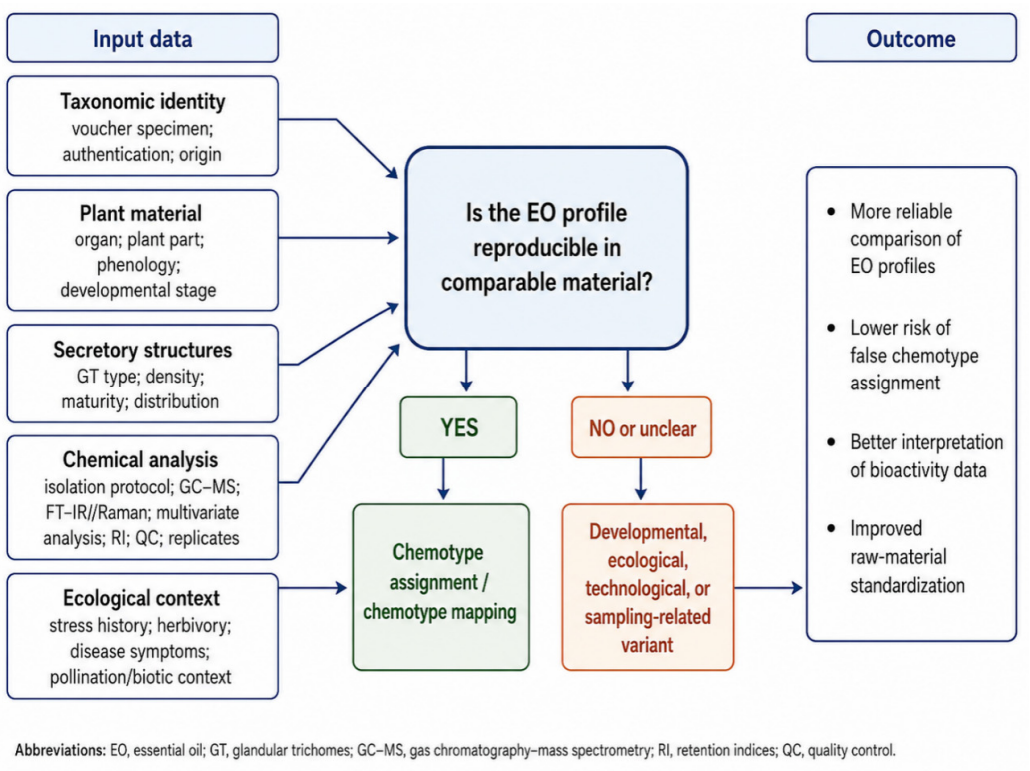

Figure 2: Plant-centered decision workflow for interpreting essential-oil variability. Taxonomic authentication, plant-material definition, secretory-structure phenotyping, standardized EO isolation and chemical profiling, including GC–MS, RI/QC control, optional FT-IR/Raman fingerprinting and multivariate analysis, and minimal ecological metadata are combined to assess whether an observed profile represents a reproducible chemotype or a developmental, environmental, biotic, technological, or sampling-related variant. Abbreviations: EO, essential oil; GT, glandular trichomes; GC–MS, gas chromatography–mass spectrometry; FT-IR, Fourier-transform infrared spectroscopy; RI, retention indices; QC, quality control.

The workflow is intended as a decision aid rather than an additional descriptive layer. It asks whether a chemical profile is reproducible in botanically and technologically comparable material before it is assigned chemotype status [75,76,81]. By linking chemical profiling with voucher-based authentication, organ and phenology data, secretory-structure information, and minimal ecological metadata, the framework reduces the risk of false chemotype assignment and improves comparison of EO bioactivity across

studies [17,24,48,49,72]. The main determinants and recommended measurements are summarized in Table 2.

Table 2: Botanical Determinants → Expected Shifts in EO Composition → Recommended Measurements.

Botanical Determinant	Expected Shift in EO	Recommended Measurements/Metadata
Species identification and taxonomy	"False" chemotypic differences due to misidentification	Voucher specimen, taxonomic verification, optionally barcode; origin
Organ (leaf/flower/inflorescence/seeds)	Changes in the proportions of terpenes and oxygenated compounds; disappearance/appearance of markers	Record of organ + stage; organ-specific replicates
Traits of secretory structures (GT density, distribution)	Change in yield; shifts in monoterpenes/oxygenated terpenes	LM/SEM; GT density mapping; histochemistry
Development and phenology	Temporal changes in dominant constituents and minor fractions	Phenological scale; time series; constant harvest time
Abiotic stress	Induction/inhibition of certain terpenoids; change in degree of oxidation	Microclimate logs; stress measures; water status
Biotic interactions (herbivory, pathogens, pollination)	Induced VOC/EO changes; variable bioactivity (mixture effects)	Herbivory/pollination history; damage scoring; monitoring
Origin and cultivation	Variability between batches/habitats; chemotypic shifts	Agrotechnical data; soil/fertilization; origin documentation
Extraction and analytics	Apparent differences (methodological artifacts)	Standardization of isolation; RI; internal standards; QC
Stereochemistry	The same "main" constituent, but a different enantiomeric ratio and activity	Chiral GC; reporting of ratios

Table prepared on the basis of the synthesis of data discussed in Sections 3–7.

Future Directions

(1) Climate change and the "new geography of chemotypes".

Progressive warming, changes in precipitation regimes, heat waves, and intensifying episodes of drought will substantially modulate the biosynthesis and accumulation of terpenoids in aromatic plants. In botanical terms, "chemotypes" observed today in a given region may shift, and former correlations between habitat and EO composition may require revision. Consequently, multi-year data series, with microclimate and phenology metadata, will be needed to distinguish short-term variability from persistent environmental trends [4,176–178].

(2) Chemotype mapping: from local descriptions to globally comparable atlases.

Many taxa lack coherent, comparable chemotype maps that would link EO composition with botanical authentication, organ, and analytical standard. A solution may be the development of "chemotype atlases" based on harmonized protocols, RI reporting, QC, botanical metadata, and chemometrics, enabling comparisons between centers and regions [50,72]. Such mapping has value not only taxonomically and ecologically, but also applicatively, including raw material selection, batch standardization, and targeted cultivation [72,153,171,173].

(3) Multi-omics and the biology of secretory structures: from correlation to mechanism.

The next step in EO studies is the transition from correlating composition with environmental conditions to identifying regulatory mechanisms: TPS/P450 expression, control of MEP/MVA precursor flux, and the physiology of secretory cells. Multi-omics approaches (transcriptomics, proteomics, metabolomics) and cell type-specific analyses, for example GT, may enable a mechanistic explanation of chemotype formation and plasticity [24,27,37,38,42]. From an application perspective, this opens the way to more rational selection of cultivars and cultivation practices, as well as to stabilization of the EO profile without loss of biological diversity.

In conclusion, the plant-centered framework proposed here does not replace chemical profiling, but strengthens its interpretation by embedding EO composition in the biology, development, and ecology of the plant source.

Acknowledgement: During manuscript preparation, the author used ChatGPT (OpenAI) solely for language editing, translation support, and preliminary visual organization of schematic figures. All scientific content, citations, interpretations, and final wording were critically revised and verified by the author, who accepts full responsibility for the final content of the manuscript.

Funding Statement: The author received no specific funding for this study.

Availability of Data and Materials: No new data were created or analyzed in this study. Data sharing is not applicable.

Ethics Approval: Not applicable.

Conflicts of Interest: The author declares no conflicts of interest.

Abbreviations

EO	essential oil
VOC(s)	volatile organic compound(s)
GT	glandular trichome(s)
LM	light microscopy
SEM	scanning electron microscopy
MEP	2-C-methyl-D-erythritol 4-phosphate pathway
MVA	mevalonate pathway
IPP	isopentenyl diphosphate
DMAPP	dimethylallyl diphosphate
GPP	geranyl diphosphate
NPP	neryl diphosphate
FPP	farnesyl diphosphate
TPS	terpene synthase(s)
P450	cytochrome P450 monooxygenase(s)
GC–MS	gas chromatography–mass spectrometry
FT-IR	Fourier-transform infrared spectroscopy
RI	retention index/indices
QC	quality control
PCA	principal component analysis
HCA	hierarchical cluster analysis
SAR	structure–activity relationship

References

1. Burt S. Essential oils: their antibacterial properties and potential applications in foods—a review. Int J Food Microbiol. 2004;94(3):223–53. [CrossRef].
2. Hérent MF, De Bie V, Tilquin B. Determination of new retention indices for quick identification of essential oils compounds. J Pharm Biomed Anal. 2007;43(3):886–92. [CrossRef].
3. Dudareva N, Klempien A, Muhlemann JK, Kaplan I. Biosynthesis, function and metabolic engineering of plant volatile organic compounds. New Phytol. 2013;198(1):16–32. [CrossRef].
4. Schuman MC. Where, when, and why do plant volatiles mediate ecological signaling? The answer is blowing in the wind. Annu Rev Plant Biol. 2023;74:609–33. [CrossRef].
5. Figueiredo AC, Barroso JG, Pedro LG, Scheffer JJC. Factors affecting secondary metabolite production in plants: volatile components and essential oils. Flavour Fragr J. 2008;23(4):213–26. [CrossRef].
6. Sangwan NS, Farooqi AHA, Shabih F, Sangwan RS. Regulation of essential oil production in plants. Plant Growth Regul. 2001;34(1):3–21. [CrossRef].
7. Tholl D. Biosynthesis and biological functions of terpenoids in plants. In: Biotechnology of isoprenoids. Cham, Switzerland: Springer; 2015. p. 63–106. [CrossRef].
8. Gang DR, Wang J, Dudareva N, Nam KH, Simon JE, Lewinsohn E, et al. An investigation of the storage and biosynthesis of phenylpropenes in sweet basil. Plant Physiol. 2001;125(2):539–55. [CrossRef].
9. McConkey ME, Gershenzon J, Croteau RB. Developmental regulation of monoterpene biosynthesis in the glandular trichomes of peppermint. Plant Physiol. 2000;122(1):215–24. [CrossRef].
10. Lange BM, Wildung MR, Stauber EJ, Sanchez C, Pouchnik D, Croteau R. Probing essential oil biosynthesis and secretion by functional evaluation of expressed sequence tags from mint glandular trichomes. Proc Natl Acad Sci U S A. 2000;97(6):2934–9. [CrossRef].
11. Xiang S, Zhou S, Deng X, Zhang F. Plant epidermis-derived secretory structures: from glandular trichomes to secretory cavities. New Phytol. 2026;249(6):2714–21. [CrossRef].
12. Wang G, Tian L, Aziz N, Broun P, Dai X, He J, et al. Terpene biosynthesis in glandular trichomes of hop. Plant Physiol. 2008;148(3):1254–66. [CrossRef].
13. Akhtar MQ, Qamar N, Yadav P, Kulkarni P, Kumar A, Shasany AK. Comparative glandular trichome transcriptome-based gene characterization reveals reasons for differential (−)-menthol biosynthesis in *Mentha* species. Physiol Plant. 2017;160(2):128–41. [CrossRef].
14. Sarker LS, Galata M, Demissie ZA, Mahmoud SS. Molecular cloning and functional characterization of borneol dehydrogenase from the glandular trichomes of *Lavandula x intermedia*. Arch Biochem Biophys. 2012;528(2):163–70. [CrossRef].
15. Huang M, Abel C, Sohrabi R, Petri J, Haupt I, Cosimano J, et al. Variation of herbivore-induced volatile terpenes among Arabidopsis ecotypes depends on allelic differences and subcellular targeting of two terpene synthases, TPS02 and TPS03. Plant Physiol. 2010;153(3):1293–310. [CrossRef].
16. Yu X, Qi X, Li S, Fang H, Bai Y, Li L, et al. Transcriptome analysis of light-regulated monoterpenes biosynthesis in leaves of *Mentha canadensis* L. Plants. 2021;10(5):930. [CrossRef].
17. Camina JL, Usseglio V, Marquez V, Merlo C, Dambolena JS, Zygadlo JA, et al. Ecological interactions affect the bioactivity of medicinal plants. Sci Rep. 2023;13(1):12165. [CrossRef].
18. Page MJ, McKenzie JE, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, et al. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. BMJ. 2021:n71. [CrossRef].
19. Rethlefsen ML, Kirtley S, Waffenschmidt S, Ayala AP, Moher D, Page MJ, et al. PRISMA-S: an extension to the PRISMA statement for reporting literature searches in systematic reviews. Syst Rev. 2021;10(1):39. [CrossRef].
20. Baethge C, Goldbeck-Wood S, Mertens S. SANRA—a scale for the quality assessment of narrative review articles. Res Integr Peer Rev. 2019;4(1):5. [CrossRef].
21. Schuurink R, Tissier A. Glandular trichomes: micro-organs with model status? New Phytol. 2020;225(6):2251–66. [CrossRef].
22. Ascensão L, Mota L, Castro M. Glandular trichomes on the leaves and flowers of *Plectranthus ornatus*: morphology, distribution and histochemistry. Ann Bot. 1999;84(4):437–47. [CrossRef].
23. Tissier A. Glandular trichomes: what comes after expressed sequence tags? Plant J. 2012;70(1):51–68. [CrossRef].

24. Mahmoud SS, Maddock S, Adal AM. Isoprenoid metabolism and engineering in glandular trichomes of Lamiaceae. Front Plant Sci. 2021;12:699157. [CrossRef].
25. Glas JJ, Schimmel BC, Alba JM, Escobar-Bravo R, Schuurink RC, Kant MR. Plant glandular trichomes as targets for breeding or engineering of resistance to herbivores. Int J Mol Sci. 2012;13(12):17077–103. [CrossRef].
26. Lange BM, Turner GW. Terpenoid biosynthesis in trichomes—current status and future opportunities. Plant Biotechnol J. 2013;11(1):2–22. [CrossRef].
27. Johnson SR, Lange I, Srividya N, Lange BM. Bioenergetics of monoterpenoid essential oil biosynthesis in nonphotosynthetic glandular trichomes. Plant Physiol. 2017;175(2):681–95. [CrossRef].
28. Turner GW, Croteau R. Organization of monoterpene biosynthesis in Mentha. Immunocytochemical localizations of geranyl diphosphate synthase, limonene-6-hydroxylase, isopiperitenol dehydrogenase, and pulegone reductase. Plant Physiol. 2004;136(4):4215–27. [CrossRef].
29. Turner GW, Gershenzon J, Croteau RB. Development of peltate glandular trichomes of peppermint. Plant Physiol. 2000;124(2):665–80. [CrossRef].
30. Schilmiller AL, Schauvinhold I, Larson M, Xu R, Charbonneau AL, Schmidt A, et al. Monoterpenes in the glandular trichomes of tomato are synthesized from a neryl diphosphate precursor rather than geranyl diphosphate. Proc Natl Acad Sci U S A. 2009;106(26):10865–70. [CrossRef].
31. Bergau N, Bennewitz S, Syrowatka F, Hause G, Tissier A. The development of type VI glandular trichomes in the cultivated tomato *Solanum lycopersicum* and a related wild species *S. habrochaites*. BMC Plant Biol. 2015;15:289. [CrossRef].
32. Xu J, van Herwijnen ZO, Dräger DB, Sui C, Haring MA, Schuurink RC. SlMYC1 regulates type VI glandular trichome formation and terpene biosynthesis in tomato glandular cells. Plant Cell. 2018;30(12):2988–3005. [CrossRef].
33. Xie Z, Kapteyn J, Gang DR. A systems biology investigation of the MEP/terpenoid and shikimate/phenylpropanoid pathways points to multiple levels of metabolic control in sweet basil glandular trichomes. Plant J. 2008;54(3):349–61. [CrossRef].
34. Gershenzon J, McCaskill D, Rajaonarivony JI, Mihaliak C, Karp F, Croteau R. Isolation of secretory cells from plant glandular trichomes and their use in biosynthetic studies of monoterpenes and other gland products. Anal Biochem. 1992;200(1):130–8. [CrossRef].
35. Rodrigues L, Póvoa O, Teixeira G, Figueiredo AC, Moldão M, Monteiro A. Trichomes micromorphology and essential oil variation at different developmental stages of cultivated and wild growing *Mentha pulegium* L. populations from Portugal. Ind Crops Prod. 2013;43:692–700. [CrossRef].
36. de Souza MAA, dos Santos LA, de Brito DMC, Rocha JF, Castro RN, Fernandes MS, et al. Influence of light intensity on glandular trichome density, gene expression and essential oil of menthol mint (*Mentha arvensis* L.). J Essent Oil Res. 2016;28(2):138–45. [CrossRef].
37. Bergau N, Navarette Santos A, Henning A, Balcke GU, Tissier A. Autofluorescence as a signal to sort developing glandular trichomes by flow cytometry. Front Plant Sci. 2016;7:949. [CrossRef].
38. Zhang M, Li M, An Y, Liu C, Zhao Q, Zhang D, et al. Single-nucleus transcriptomics reveal the morphogenesis and artemisinin biosynthesis in *Artemisia annua* glandular trichomes. Nat Commun. 2025;16:8646. [CrossRef].
39. Chen M, Yan T, Shen Q, Lu X, Pan Q, Huang Y, et al. Glandular trichome-specific WRKY 1 promotes artemisinin biosynthesis in *Artemisia annua*. New Phytol. 2017;214(1):304–16. [CrossRef].
40. Tan H, Xiao L, Gao S, Li Q, Chen J, Xiao Y, et al. Trichome and artemisinin regulator 1 is required for trichome development and artemisinin biosynthesis in *Artemisia annua*. Mol Plant. 2015;8(9):1396–411. [CrossRef].
41. Wu T, Wang Y, Guo D. Investigation of glandular trichome proteins in *Artemisia annua* L. using comparative proteomics. PLoS One. 2012;7(8):e41822. [CrossRef].
42. Zhou P, Chen H, Dang J, Shi Z, Shao Y, Liu C, et al. Single-cell transcriptome of *Nepeta tenuifolia* leaves reveal differentiation trajectories in glandular trichomes. Front Plant Sci. 2022;13:988594. [CrossRef].
43. Weckerle CS, de Boer HJ, Puri RK, van Andel T, Bussmann RW, Leonti M. Recommended standards for conducting and reporting ethnopharmacological field studies. J Ethnopharmacol. 2018;210:125–32. [CrossRef].
44. Cook D, Lee ST, Gardner DR, Molyneux RJ, Johnson RL, Taylor CM. Use of herbarium voucher specimens to investigate phytochemical composition in poisonous plant research. J Agric Food Chem. 2021;69(14):4037–47. [CrossRef].

45. Hildreth J, Hrabeta-Robinson E, Applequist W, Betz J, Miller J. Standard operating procedure for the collection and preparation of voucher plant specimens for use in the nutraceutical industry. Anal Bioanal Chem. 2007;389(1):13–7. [CrossRef].
46. European Medicines Agency, Committee on Herbal Medicinal Products (HMPC). European Union herbal monograph on *Salvia officinalis* L., folium. Amsterdam, The Netherlands: European Medicines Agency; 2016.
47. ISO 9235:2021. Aromatic natural raw materials—vocabulary. Geneva, Switzerland: International Organization for Standardization; 2021.
48. Tozin LR, Marques MO, Rodrigues TM. Glandular trichome density and essential oil composition in leaves and inflorescences of *Lippia origanoides* Kunth (Verbenaceae) in the Brazilian Cerrado. An Acad Bras Cienc. 2015;87(2):943–53. [CrossRef].
49. Ložienė K. Peltate glandular trichomes in relation to their parameters, essential oil amount, chemotype, plant sex and habitat characteristics in thymus pulegioides. Horticulturae. 2025;11(8):871. [CrossRef].
50. Papoutsoglou EA, Faria D, Arend D, Arnaud E, Athanasiadis IN, Chaves I, et al. Enabling reusability of plant phenomic datasets with MIAPPE 1.1. New Phytol. 2020;227(1):260–73. [CrossRef].
51. Hussain AI, Anwar F, Hussain Sherazi ST, Przybylski R. Chemical composition, antioxidant and antimicrobial activities of basil (*Ocimum basilicum*) essential oils depends on seasonal variations. Food Chem. 2008;108(3):986–95. [CrossRef].
52. Hazrati S, Beidaghi P, Beyraghdar Kashkooli A, Hosseini SJ, Nicola S. Effect of harvesting time variations on essential oil yield and composition of sage (*Salvia officinalis*). Horticulturae. 2022;8(2):149. [CrossRef].
53. Calín-Sánchez Á, Figiel A, Lech K, Szumny A, Carbonell-Barrachina ÁA. Effects of drying methods on the composition of thyme (*Thymus vulgaris* L.) essential oil. Dry Technol. 2013;31(2):224–35. [CrossRef].
54. Ćavar Zeljković S, Smékalová K, Kaffková K, Štefelová N. Influence of post-harvesting period on quality of thyme and spearmint essential oils. J Appl Res Med Aromat Plants. 2021;25:100335. [CrossRef].
55. Cannon JB, Cantrell CL, Astatkie T, Zheljazkov VD. Modification of yield and composition of essential oils by distillation time. Ind Crops Prod. 2013;41:214–20. [CrossRef].
56. Zheljazkov VD, Cantrell CL, Astatkie T, Jeliazkova E. Distillation time effect on lavender essential oil yield and composition. J Oleo Sci. 2013;62(4):195–9. [CrossRef].
57. Zheljazkov VD, Astatkie T, Schlegel V. Hydrodistillation extraction time effect on essential oil yield, composition, and bioactivity of coriander oil. J Oleo Sci. 2014;63(9):857–65. [CrossRef].
58. Laule O, Fürholz A, Chang HS, Zhu T, Wang X, Heifetz PB, et al. Crosstalk between cytosolic and plastidial pathways of isoprenoid biosynthesis in *Arabidopsis thaliana*. Proc Natl Acad Sci U S A. 2003;100(11):6866–71. [CrossRef].
59. Vranová E, Coman D, Gruissem W. Network analysis of the MVA and MEP pathways for isoprenoid synthesis. Annu Rev Plant Biol. 2013;64:665–700. [CrossRef].
60. Banerjee A, Hamberger B. P450s controlling metabolic bifurcations in plant terpene specialized metabolism. Phytochem Rev. 2018;17(1):81–111. [CrossRef].
61. Hemmerlin A, Hoeffler JF, Meyer O, Tritsch D, Kagan IA, Grosdemange-Billiard C, et al. Cross-talk between the cytosolic mevalonate and the plastidial methylerythritol phosphate pathways in tobacco bright yellow-2 cells. J Biol Chem. 2003;278(29):26666–76. [CrossRef].
62. Dudareva N, Andersson S, Orlova I, Gatto N, Reichelt M, Rhodes D, et al. The nonmevalonate pathway supports both monoterpene and sesquiterpene formation in snapdragon flowers. Proc Natl Acad Sci U S A. 2005;102(3):933–8. [CrossRef].
63. Besser K, Harper A, Welsby N, Schauvinhold I, Slocombe S, Li Y, et al. Divergent regulation of terpenoid metabolism in the trichomes of wild and cultivated tomato species. Plant Physiol. 2009;149(1):499–514. [CrossRef].
64. Sallaud C, Rontein D, Onillon S, Jabès F, Duffé P, Giacalone C, et al. A novel pathway for sesquiterpene biosynthesis from *Z,Z*-farnesyl pyrophosphate in the wild tomato *Solanum habrochaites*. Plant Cell. 2009;21(1):301–17. [CrossRef].
65. Zhang Y, Jiao D, Shen C, Zhou J, Guo J, Yang J, et al. Plant prenyltransferases: diversity, catalytic activities, mechanisms, and application in heterologous production of prenylated natural products. J Integr Plant Biol. 2026;68(4):869–902. [CrossRef].

66. Kopcsayová D, Vranová E. Functional gene network of prenyltransferases in *Arabidopsis thaliana*. Molecules. 2019;24(24):4556. [CrossRef].
67. Degenhardt J, Köllner TG, Gershenzon J. Monoterpene and sesquiterpene synthases and the origin of terpene skeletal diversity in plants. Phytochemistry. 2009;70(15–16):1621–37. [CrossRef].
68. Christianson DW. Structural and chemical biology of terpenoid cyclases. Chem Rev. 2017;117(17):11570–648. [CrossRef].
69. Bak S, Beisson F, Bishop G, Hamberger B, Höfer R, Paquette S, et al. Cytochromes P450. Arabidopsis Book. 2011;9:e0144. [CrossRef].
70. Mizutani M, Sato F. Unusual P450 reactions in plant secondary metabolism. Arch Biochem Biophys. 2011;507(1):194–203. [CrossRef].
71. Lupien S, Karp F, Wildung M, Croteau R. Regiospecific cytochrome P450 limonene hydroxylases from mint (*Mentha*) species: cDNA isolation, characterization, and functional expression of (−)-4S-limonene-3-hydroxylase and (−)-4S-limonene-6-hydroxylase. Arch Biochem Biophys. 1999;368(1):181–92. [CrossRef].
72. Rodríguez-Solana R, Daferera DJ, Mitsi C, Trigas P, Polissiou M, Tarantilis PA. Comparative chemotype determination of *Lamiaceae* plants by means of GC–MS, FT-IR, and dispersive-Raman spectroscopic techniques and GC-FID quantification. Ind Crops Prod. 2014;62:22–33. [CrossRef].
73. Thompson JD, Manicacci D. Thirty-five years of thyme: a tale of two polymorphisms. BioScience. 1998;48(10):805–15. [CrossRef].
74. Gouyon PH, Vernet P, Guillerm JL, Valdeyron G. Polymorphisms and environment: the adaptive value of the oil polymorphisms in *Thymus vulgaris* L. Heredity. 1986;57(1):59–66. [CrossRef].
75. Polatoglu K. "Chemotypes"–a fact that should not be ignored in natural product studies. Nat Prod J. 2013;3(1):10–4. [CrossRef].
76. Keefover-Ring K, Thompson JD, Linhart YB. Beyond six scents: defining a seventh *Thymus vulgaris* chemotype new to southern France by ethanol extraction. Flavour Fragr J. 2009;24(3):117–22. [CrossRef].
77. Gostin IN, Blidar CF. Glandular trichomes and essential oils variability in species of the genus *Phlomis* L.: a review. Plants. 2024;13(10):1338. [CrossRef].
78. Crocoll C, Asbach J, Novak J, Gershenzon J, Degenhardt J. Terpene synthases of oregano (*Origanum vulgare* L.) and their roles in the pathway and regulation of terpene biosynthesis. Plant Mol Biol. 2010;73(6):587–603. [CrossRef].
79. Keskitalo M, Pehu E, Simon JE. Variation in volatile compounds from tansy (*Tanacetum vulgare* L.) related to genetic and morphological differences of genotypes. Biochem Syst Ecol. 2001;29(3):267–85. [CrossRef].
80. Thompson JD, Chalchat JC, Michet A, Linhart YB, Ehlers B. Qualitative and quantitative variation in monoterpene co-occurrence and composition in the essential oil of *Thymus vulgaris* chemotypes. J Chem Ecol. 2003;29(4):859–80. [CrossRef].
81. Dussarrat T, Schweiger R, Ziaja D, Nguyen TTN, Krause L, Jakobs R, et al. Influences of chemotype and parental genotype on metabolic fingerprints of tansy plants uncovered by predictive metabolomics. Sci Rep. 2023;13:11645. [CrossRef].
82. Hudaib M, Speroni E, Di Pietra AM, Cavrini V. GC/MS evaluation of thyme (*Thymus vulgaris* L.) oil composition and variations during the vegetative cycle. J Pharm Biomed Anal. 2002;29(4):691–700. [CrossRef].
83. Dragland S, Rohloff J, Mordal R, Iversen TH. Harvest regimen optimization and essential oil production in five tansy (*Tanacetum vulgare* L.) genotypes under a northern climate. J Agric Food Chem. 2005;53(12):4946–53. [CrossRef].
84. Ložienė K, Venskutonis PR. Influence of environmental and genetic factors on the stability of essential oil composition of *Thymus pulegioides*. Biochem Syst Ecol. 2005;33(5):517–25. [CrossRef].
85. Vaičiulytė V, Ložienė K, Taraškevičius R. Impact of edaphic and climatic factors on *Thymus pulegioides* essential oil composition and potential prevalence of chemotypes. Plants. 2022;11(19):2536. [CrossRef].
86. Thompson J, Charpentier A, Bouguet G, Charmasson F, Roset S, Buatois B, et al. Evolution of a genetic polymorphism with climate change in a Mediterranean landscape. Proc Natl Acad Sci U S A. 2013;110(8):2893–7. [CrossRef].
87. Linhart YB, Thompson JD. Terpene-based selective herbivory by *Helix aspersa* (Mollusca) on *Thymus vulgaris* (Labiatae). Oecologia. 1995;102(1):126–32. [CrossRef].

88. Linhart YB, Keefover-Ring K, Mooney KA, Breland B, Thompson JD. A chemical polymorphism in a multitrophic setting: thyme monoterpene composition and food web structure. Am Nat. 2005;166(4):517–29. [CrossRef].
89. Gershenzon J, Dudareva N. The function of terpene natural products in the natural world. Nat Chem Biol. 2007;3(7):408–14. [CrossRef].
90. Dicke M, Baldwin IT. The evolutionary context for herbivore-induced plant volatiles: beyond the 'cry for help'. Trends Plant Sci. 2010;15(3):167–75. [CrossRef].
91. Arimura G, Matsui K, Takabayashi J. Chemical and molecular ecology of herbivore-induced plant volatiles: proximate factors and their ultimate functions. Plant Cell Physiol. 2009;50(5):911–23. [CrossRef].
92. Bakkali F, Averbeck S, Averbeck D, Idaomar M. Biological effects of essential oils—a review. Food Chem Toxicol. 2008;46(2):446–75. [CrossRef].
93. Unsicker SB, Kunert G, Gershenzon J. Protective perfumes: the role of vegetative volatiles in plant defense against herbivores. Curr Opin Plant Biol. 2009;12(4):479–85. [CrossRef].
94. Mumm R, Hilker M. Direct and indirect chemical defence of pine against folivorous insects. Trends Plant Sci. 2006;11(7):351–8. [CrossRef].
95. Hyldgaard M, Mygind T, Meyer RL. Essential oils in food preservation: mode of action, synergies, and interactions with food matrix components. Front Microbiol. 2012;3:12. [CrossRef].
96. Bassolé IH, Juliani HR. Essential oils in combination and their antimicrobial properties. Molecules. 2012;17(4):3989–4006. [CrossRef].
97. Aharoni A, Giri AP, Deuerlein S, Griepink F, de Kogel WJ, Verstappen FWA, et al. Terpenoid metabolism in wild-type and transgenic Arabidopsis plants. Plant Cell. 2003;15(12):2866–84. [CrossRef].
98. Schiestl FP. The evolution of floral scent and insect chemical communication. Ecol Lett. 2010;13(5):643–56. [CrossRef].
99. Kellenberger RT, Schlüter PM, Schiestl FP. Herbivore-Induced DNA demethylation changes floral signalling and attractiveness to pollinators in *Brassica rapa*. PLoS One. 2016;11(11):e0166646. [CrossRef].
100. De Moraes CM, Lewis WJ, Paré PW, Alborn HT, Tumlinson JH. Herbivore-infested plants selectively attract parasitoids. Nature. 1998;393(6685):570–3. [CrossRef].
101. Turlings TC, Tumlinson JH, Lewis WJ. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. Science. 1990;250(4985):1251–3. [CrossRef].
102. Kessler A, Baldwin IT. Defensive function of herbivore-induced plant volatile emissions in nature. Science. 2001;291(5511):2141–4. [CrossRef].
103. Mumm R, Dicke M. Variation in natural plant products and the attraction of bodyguards involved in indirect plant defense. Can J Zool. 2010;88(7):628–67. [CrossRef].
104. Allmann S, Baldwin IT. Insects betray themselves in nature to predators by rapid isomerization of green leaf volatiles. Science. 2010;329(5995):1075–8. [CrossRef].
105. Engelberth J, Alborn HT, Schmelz EA, Tumlinson JH. Airborne signals prime plants against insect herbivore attack. Proc Natl Acad Sci U S A. 2004;101(6):1781–5. [CrossRef].
106. Schuman MC, Barthel K, Baldwin IT. Herbivory-induced volatiles function as defenses increasing fitness of the native plant *Nicotiana attenuata* in nature. Elife. 2012;1:e00007. [CrossRef].
107. Joo Y, Schuman MC, Goldberg JK, Kim SG, Yon F, Brütting C, et al. Herbivore-induced volatile blends with both "fast" and "slow" components provide robust indirect defence in nature. Funct Ecol. 2018;32(1):136–49. [CrossRef].
108. Joo Y, Schuman MC, Goldberg JK, Wissgott A, Kim SG, Baldwin IT. Herbivory elicits changes in green leaf volatile production via jasmonate signaling and the circadian clock. Plant Cell Environ. 2019;42(3):972–82. [CrossRef].
109. Tholl D, Boland W, Hansel A, Loreto F, Röse USR, Schnitzler JP. Practical approaches to plant volatile analysis. Plant J. 2006;45(4):540–60. [CrossRef].
110. Adler LS. The ecological significance of toxic nectar. Oikos. 2000;91(3):409–20. [CrossRef].
111. Raguso RA. Wake up and smell the roses: the ecology and evolution of floral scent. Annu Rev Ecol Evol Syst. 2008;39:549–69. [CrossRef].
112. Burkle LA, Runyon JB. Drought and leaf herbivory influence floral volatiles and pollinator attraction. Glob Change Biol. 2016;22(4):1644–54. [CrossRef].

113. Schiestl FP, Kirk H, Bigler L, Cozzolino S, Desurmont GA. Herbivory and floral signaling: phenotypic plasticity and tradeoffs between reproduction and indirect defense. New Phytol. 2014;203(1):257–66. [CrossRef].
114. Kessler A, Halitschke R, Poveda K. Herbivory-mediated pollinator limitation: negative impacts of induced volatiles on plant-pollinator interactions. Ecology. 2011;92(9):1769–80. [CrossRef].
115. Theis N, Lerdau M, Raguso RA. The challenge of attracting pollinators while evading floral herbivores: patterns of fragrance emission in *Cirsium arvense* and *Cirsium repandum* (Asteraceae). Int J Plant Sci. 2007;168(5):587–601. [CrossRef].
116. Kessler A, Halitschke R. Testing the potential for conflicting selection on floral chemical traits by pollinators and herbivores: predictions and case study. Funct Ecol. 2009;23(5):901–12. [CrossRef].
117. Brosset A, Blande JD. Volatile-mediated plant-plant interactions: volatile organic compounds as modulators of receiver plant defence, growth, and reproduction. J Exp Bot. 2022;73(2):511–28. [CrossRef].
118. Ninkovic V, Markovic D, Rensing M. Plant volatiles as cues and signals in plant communication. Plant Cell Environ. 2021;44(4):1030–43. [CrossRef].
119. Heil M, Karban R. Explaining evolution of plant communication by airborne signals. Trends Ecol Evol. 2010;25(3):137–44. [CrossRef].
120. Pierik R, Ballaré CL, Dicke M. Ecology of plant volatiles: taking a plant community perspective. Plant Cell Environ. 2014;37(8):1845–53. [CrossRef].
121. Meents AK, Mithöfer A. Plant-plant communication: is there a role for volatile damage-associated molecular patterns? Front Plant Sci. 2020;11:583275. [CrossRef].
122. Schuman MC, Allmann S, Baldwin IT. Plant defense phenotypes determine the consequences of volatile emission for individuals and neighbors. Elife. 2015;4:e04490. [CrossRef].
123. Pavarini DP, Pavarini SP, Niehues M, Lopes NP. Exogenous influences on plant secondary metabolite levels. Anim Feed Sci Technol. 2012;176(1–4):5–16. [CrossRef].
124. Ncube B, Finnie JF, Van Staden J. Quality from the field: the impact of environmental factors as quality determinants in medicinal plants. S Afr J Bot. 2012;82:11–20. [CrossRef].
125. Jansen RMC, Wildt J, Kappers IF, Bouwmeester HJ, Hofstee JW, van Henten EJ. Detection of diseased plants by analysis of volatile organic compound emission. Annu Rev Phytopathol. 2011;49:157–74. [CrossRef].
126. Mithöfer A, Boland W. Plant defense against herbivores: chemical aspects. Annu Rev Plant Biol. 2012;63:431–50. [CrossRef].
127. Johnson MTJ, Bertrand JA, Turcotte MM. Precision and accuracy in quantifying herbivory. Ecol Entomol. 2016;41(1):112–21. [CrossRef].
128. Bock CH, Poole GH, Parker PE, Gottwald TR. Plant disease severity estimated visually, by digital photography and image analysis, and by hyperspectral imaging. Crit Rev Plant Sci. 2010;29(2):59–107. [CrossRef].
129. Calo JR, Crandall PG, O'Bryan CA, Ricke SC. Essential oils as antimicrobials in food systems—a review. Food Control. 2015;54:111–9. [CrossRef].
130. Ruberto G, Baratta MT. Antioxidant activity of selected essential oil components in two lipid model systems. Food Chem. 2000;69(2):167–74. [CrossRef].
131. Abd-ElGawad AM, El Gendy AEG, Assaeed AM, Al-Rowaily SL, Alharthi AS, Mohamed TA, et al. Phytotoxic effects of plant essential oils: a systematic review and structure-activity relationship based on chemometric analyses. Plants. 2020;10(1):36. [CrossRef].
132. Matera R, Lucchi E, Valgimigli L. Plant essential oils as healthy functional ingredients of nutraceuticals and diet supplements: a review. Molecules. 2023;28(2):901. [CrossRef].
133. Chávez-Delgado EL, Jacobo-Velázquez DA. Essential oils: recent advances on their dual role as food preservatives and nutraceuticals against the metabolic syndrome. Foods. 2023;12(5):1079. [CrossRef].
134. Perricone M, Arace E, Corbo MR, Sinigaglia M, Bevilacqua A. Bioactivity of essential oils: a review on their interaction with food components. Front Microbiol. 2015;6:76. [CrossRef].
135. Brenna E, Fuganti C, Serra S. Enantioselective perception of chiral odorants. Tetrahedron Asymmetry. 2003;14(1):1–42. [CrossRef].

136. Guadayol M, Guadayol JM, Vendrell E, Collgrós F, Caixach J. Relationship between the terpene enantiomeric distribution and the growth cycle of lemon fruit and comparison of two extraction methods. J Essent Oil Res. 2018;30(4):244–52. [CrossRef].
137. König WA, Hochmuth DH. Enantioselective gas chromatography in flavor and fragrance analysis: strategies for the identification of known and unknown plant volatiles. J Chromatogr Sci. 2004;42(8):423–39. [CrossRef].
138. Guimarães AC, Meireles LM, Lemos MF, Guimarães MCC, Endringer DC, Fronza M, et al. Antibacterial activity of terpenes and terpenoids present in essential oils. Molecules. 2019;24(13):2471. [CrossRef].
139. Miladinović DL, Dimitrijević MV, Mihajilov-Krstev TM, Marković MS, Ćirić VM. The significance of minor components on the antibacterial activity of essential oil via chemometrics. LWT. 2021;136:110305. [CrossRef].
140. Lambert RJW, Skandamis PN, Coote PJ, Nychas GJE. A study of the minimum inhibitory concentration and mode of action of oregano essential oil, thymol and carvacrol. J Appl Microbiol. 2001;91(3):453–62. [CrossRef].
141. Gill AO, Holley RA. Disruption of *Escherichia coli*, *Listeria monocytogenes* and *Lactobacillus sakei* cellular membranes by plant oil aromatics. Int J Food Microbiol. 2006;108(1):1–9. [CrossRef].
142. Gutierrez J, Barry-Ryan C, Bourke P. The antimicrobial efficacy of plant essential oil combinations and interactions with food ingredients. Int J Food Microbiol. 2008;124(1):91–7. [CrossRef].
143. Milos M, Makota D. Investigation of antioxidant synergisms and antagonisms among thymol, carvacrol, thymoquinone and p-cymene in a model system using the Briggs–Rauscher oscillating reaction. Food Chem. 2012;131(1):296–9. [CrossRef].
144. de Martino L, Mancini E, de Almeida LF, de Feo V. The antigerminative activity of twenty-seven monoterpenes. Molecules. 2010;15(9):6630–7. [CrossRef].
145. Chaimovitsh D, Shachter A, Abu-Abied M, Rubin B, Sadot E, Dudai N. Herbicidal activity of monoterpenes is associated with disruption of microtubule functionality and membrane integrity. Weed Sci. 2017;65(1):19–30. [CrossRef].
146. Werrie PY, Durenne B, Delaplace P, Fauconnier ML. Phytotoxicity of essential oils: opportunities and constraints for the development of biopesticides. A review. Foods. 2020;9(9):1291. [CrossRef].
147. Lins L, Dal Maso S, Foncoux B, Kamili A, Laurin Y, Genva M, et al. Insights into the relationships between herbicide activities, molecular structure and membrane interaction of cinnamon and citronella essential oils components. Int J Mol Sci. 2019;20(16):4007. [CrossRef].
148. Aribi-Zouioueche L, Couic-Marinier F. Huiles essentielles et chiralité moléculaire. Comptes Rendus Chim. 2021;24(3):397–414. [CrossRef].
149. de Sousa DP, Nóbrega FF, Santos CC, de Almeida RN. Anticonvulsant activity of the linalool enantiomers and racemate: investigation of chiral influence. Nat Prod Commun. 2010;5(12):1847–51. [CrossRef].
150. Allenspach M, Valder C, Flamm D, Steuer C. Authenticity control of pine sylvestris essential oil by chiral gas chromatographic analysis of α-pinene. Sci Rep. 2021;11:16923. [CrossRef].
151. Sanzini E, Badea M, Dos Santos A, Restani P, Sievers H. Quality control of plant food supplements. Food Funct. 2011;2(12):740. [CrossRef].
152. van Breemen RB, Fong HH, Farnsworth NR. The role of quality assurance and standardization in the safety of botanical dietary supplements. Chem Res Toxicol. 2007;20(4):577–82. [CrossRef].
153. Kowalska G, Baj T, Kowalski R. Comparison of chemical composition of essential oil acquired from single-component pharmaceutical products, food products, and from the cultivation of sage *Salvia officinalis* L. from Poland. J Essent Oil Bear Plants. 2021;24(6):1235–47. [CrossRef].
154. Raal A, Orav A, Ilina T, Kovalyova A, Koliadzhyn T, Avidzba Y, et al. Variation in the composition of the essential oil of commercial *Salvia officinalis* L. leaves samples from different countries. Phyton. 2024;93(8):2051–62. [CrossRef].
155. Länger R, Mechtler C, Jurenitsch J. Composition of the essential oils of commercial samples of *Salvia officinalis* L. and *S. fruticosa* miller: a comparison of oils obtained by extraction and steam distillation. Phytochem Anal. 1996;7(6):289–93. [CrossRef].
156. Schmiderer C, Torres-Londoño P, Novak J. Proof of geographical origin of Albanian sage by essential oil analysis. Biochem Syst Ecol. 2013;51:70–7. [CrossRef].
157. Arraiza MP, Arrabal C, Lopez JV. Seasonal variation of essential oil yield and composition of sage (*Salvia officinalis* L.) grown in Castilla-La Mancha (central Spain). Not Bot Hort Agrobot Cluj. 2012;40(2):106. [CrossRef].

158. Stengele M, Stahl-Biskup E. Seasonal variation of the essential oil of European pennyroyal (*Mentha pulegium* L.). Acta Hortic. 1993;344:41–51. [CrossRef].
159. Karray-Bouraoui N, Rabhi M, Neffati M, Baldan B, Ranieri A, Marzouk B, et al. Salt effect on yield and composition of shoot essential oil and trichome morphology and density on leaves of *Mentha pulegium*. Ind Crops Prod. 2009;30(3):338–43. [CrossRef].
160. Caputo L, Cornara L, Raimondo FM, de Feo V, Vanin S, Denaro M, et al. *Mentha pulegium* L.: a plant underestimated for its toxicity to be recovered from the perspective of the circular economy. Molecules. 2021;26(8):2154. [CrossRef].
161. Vaičiulytė V, Ložienė K, Taraškevičius R, Butkienė R. Variation of essential oil composition of *Thymus pulegioides* in relation to soil chemistry. Ind Crops Prod. 2017;95:422–33. [CrossRef].
162. Ložienė K, Vaičiulytė V. Geraniol and carvacrol in essential oil bearing *Thymus pulegioides*: distribution in natural habitats and phytotoxic effect. Molecules. 2022;27(3):986. [CrossRef].
163. Stashenko EE, Martínez JR, Ruíz CA, Arias G, Durán C, Salgar W, et al. *Lippia origanoides* chemotype differentiation based on essential oil GC-MS and principal component analysis. J Sep Sci. 2010;33(1):93–103. [CrossRef].
164. Souza LM, Fonseca FSA, Silva JCRL, Silva AM, Silva JR, Martins ER. Essential oil composition in natural population of *Lippia origanoides* (Verbenaceae) during dry and rainy seasons. Rev De Biol Trop. 2019;67(1):278–85. [CrossRef].
165. Sugier P, Jaros-Tsoj K, Jaroszuk-Ściseł J, Papazoglou EG, Alexopoulou E, Sugier D, et al. Industrial hemp Futura 75 infructescence as a source of essential oils: micromorphology, chemical profile, and yield of essential oils. Ind Crops Prod. 2025;234:121527. [CrossRef].
166. Pieracci Y, Ascrizzi R, Terreni V, Pistelli L, Flamini G, Bassolino L, et al. Essential oil of *Cannabis sativa* L: comparison of yield and chemical composition of 11 hemp genotypes. Molecules. 2021;26(13):4080. [CrossRef].
167. Ascrizzi R, Flamini G, Rossi A, Santini A, Angelini LG, Tavarini S. Inflorescence yield, essential oil composition and antioxidant activity of *Cannabis sativa* L. cv 'Futura 75' in a multilocation and on-farm study. Agriculture. 2024;14(2):1–20. [CrossRef].
168. Livingston SJ, Quilichini TD, Booth JK, Wong DCJ, Rensing KH, Laflamme-Yonkman J, et al. Cannabis glandular trichomes alter morphology and metabolite content during flower maturation. Plant J. 2020;101(1):37–56. [CrossRef].
169. Tanney CAS, Backer R, Geitmann A, Smith DL. Cannabis glandular trichomes: a cellular metabolite factory. Front Plant Sci. 2021;12:721986. [CrossRef].
170. Fiorini D, Molle A, Nabissi M, Santini G, Benelli G, Maggi F. Valorizing industrial hemp (*Cannabis sativa* L.) by-products: cannabidiol enrichment in the inflorescence essential oil optimizing sample pre-treatment prior to distillation. Ind Crops Prod. 2019;128:581–9. [CrossRef].
171. Lukas B, Schmiderer C, Novak J. Essential oil diversity of European *Origanum vulgare* L. (Lamiaceae). Phytochemistry. 2015;119:32–40. [CrossRef].
172. Russo M, Galletti GC, Bocchini P, Carnacini A. Essential oil chemical composition of wild populations of Italian oregano spice (*Origanum vulgare* ssp. hirtum (link) ietswaart): a preliminary evaluation of their use in chemotaxonomy by cluster analysis. 1. Inflorescences. J Agric Food Chem. 1998;46(9):3741–6. [CrossRef].
173. Raal A, Gontova T, Ivask A, Orav A, Koshovyi O. Yield, composition, and chemotypes of essential oils from *Origanum vulgare* L. aerial parts cultivated in different European countries. Agronomy. 2024;14(12):3046. [CrossRef].
174. Baranauskienė R, Venskutonis PR, Dambrauskienė E, Viškelis P. Harvesting time influences the yield and oil composition of *Origanum vulgare* L. ssp. vulgare and ssp. *hirtum*. Ind Crops Prod. 2013;49:43–51. [CrossRef].
175. Khan M, Khan ST, Khan M, Mousa AA, Mahmood A, Alkhathlan HZ. Chemical diversity in leaf and stem essential oils of *Origanum vulgare* L. and their effects on microbicidal activities. AMB Express. 2019;9(1):176. [CrossRef].
176. Aqeel U, Aftab T, Khan MMA, Naeem M. Regulation of essential oil in aromatic plants under changing environment. J Appl Res Med Aromat Plants. 2023;32:100441. [CrossRef].
177. Loreto F, Schnitzler JP. Abiotic stresses and induced BVOCs. Trends Plant Sci. 2010;15(3):154–66. [CrossRef].
178. Peñuelas J, Staudt M. BVOCs and global change. Trends Plant Sci. 2010;15(3):133–44. [CrossRef].