GLANDULAR TRICHOMES AS MODEL STRUCTURES IN PHYTOCHEMICAL BIOSYNTHESIS RESEARCH

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ABSTRACT

This review provides a comprehensive synthesis of the value of plant glandular trichomes—microscopic chemical factories on the plant surface—as model structures for phytochemical biosynthesis research. Based on an extensive survey of recent literature, the article first catalogues the extraordinary morphological and anatomical diversity of trichomes across taxa, linking species-, organ- and developmental stage-specific patterns to adaptive ecological strategies. It then dissects the high-flux biosynthetic routes for terpenoids, phenylpropanoids, alkaloids and unusual fatty-acid derivatives that operate within trichome cells, summarising current insights into subcellular compartmentation and metabolite trafficking. Focusing on developmental genetics, the paper clarifies how HD-ZIP IV (Wo), bHLH (SlMYC1) and MYB-like transcription factors, together with jasmonate signalling, coordinate trichome biogenesis with metabolic output. The methodological strengths of microscopy, laser-capture micro-dissection, multi-omics platforms and CRISPR-based gene editing are highlighted, underscoring their capacity to interrogate and re-engineer single-cell factories. Application-oriented sections discuss how enhanced trichome density or rewired metabolite profiles can increase innate pest resistance, optimise the yield of high-value natural products and lay the groundwork for ‘designer trichomes’ that enable sustainable in planta bioproduction. By identifying knowledge gaps—such as the need to characterise trichome-specific promoters, transporters and understudied species—the review proposes a forward-looking research agenda. Overall, it positions glandular trichomes as a unifying model for single-cell systems biology and as a versatile platform for next-generation metabolic engineering, with far-reaching implications for sustainable agriculture, pharmaceuticals and the flavour-fragrance industries. In doing so, it offers researchers not only an updated conceptual framework but also practical guidelines for translating trichome biology into tangible technological innovations.

Keywords: Glandular trichomes, Secondary metabolites, Terpenoids, Metabolic engineering, Plant defence

FİTOKİMYASAL BİYOSENTEZ ARAŞTIRMALARINDA MODEL YAPILAR OLARAK SALGI TÜYLERİ

ÖZET

Bu çalışma, bitki yüzeyinde mikroskobik kimyasal fabrikalar olarak görev yapan salgı tüylerinin (glandular trikomlar) fitokimyasal biyosentez araştırmalarındaki model değerini kapsamlı biçimde incelemektedir. Literatür taramasına dayalı olarak hazırlanan makalede, öncelikle farklı taksonomik gruplarda görülen salgı tüylerinin morfolojik ve anatomik çeşitliliği ele alınmış; tür-, organ- ve gelişim evresi-spesifik varyasyonların ekolojik uyum stratejileriyle ilişkisi tartışılmıştır. Ardından trikom hücrelerinde yüksek düzeyde işleyen terpenoid, fenilpropanoid, alkaloid ve yağ asidi türevli yolaklar ayrıntılı olarak analiz edilmiş; hücre altı bölgeleme ve metabolik trafik mekanizmaları üzerindeki son bulgular sentezlenmiştir. Gelişimsel ve hormonal kontrolün genetik temeline odaklanan makale, Wo/HD-ZIP IV, SlMYC1 ve MYB benzeri transkripsiyon faktörleri ile jasmonat sinyalinin trikom biyogenezi ve metabolit akışını nasıl eşzamanlı yönettiğini açıklığa kavuşturmuştur. Mikroskopi, laser-yakalama mikrodiseksiyon, çoklu omik (transkriptomik-proteomik-metabolomik) ve CRISPR yaklaşımlarının salgı tüyü biyolojisinde sunduğu metodolojik avantajlar vurgulanmış; bu araçların tek hücre düzeyinde metabolik mühendislik tasarımları için potansiyeli değerlendirilmiştir. Son bölümde, yükseltilmiş trikom yoğunluğu veya yeniden programlanmış metabolit profilleri sayesinde haşere direncinin artırılması, yüksek değerli doğal ürün üretiminin optimize edilmesi ve "tasarım trikomları" aracılığıyla sürdürülebilir biyoprodüksiyon senaryoları tartışılmıştır. Ayrıca, az çalışılmış türlerde trikom işlevselliğinin aydınlatılması, trikom-özgül promotörlerin keşfi ve ürün taşınımını düzenleyen taşıyıcı proteinlerin karakterizasyonu gibi gelecek araştırma gündemleri önerilmiştir. Bu yönüyle makale, sürdürülebilir tarım, eczacılık ve koku-lezzet endüstrileri için stratejik yenilik fırsatlarını ortaya koymaktadır.

Anahtar Kelimeler: Salgı tüyü, Sekonder metabolit, terpenoid, Metabolik mühendislik, Bitki savunması

1. INTRODUCTION

Plant glandular trichomes are specialized epidermal appendages that serve as microscopic chemical factories on the plant surface. Approximately one-third of all vascular plant species develop glandular trichomes (Chang et al., 2024), and these structures contribute a significant portion of a plant's secondary metabolite profile. Glandular trichomes typically consist of a stalk and a secretory head of one or more cells, and they actively synthesize, secrete, and sometimes store a diverse array of phytochemicals. These compounds include essential oils, resins, and other specialized metabolites valued as fragrances, flavors, or pharmaceuticals. Evolutionarily, many trichome-derived substances function in plant defense – deterring herbivores, inhibiting pathogens, or mitigating abiotic stresses – even though humans also exploit them for industrial uses (Glas et al., 2012). Because of their prolific biosynthetic activity and accessible location on plant surfaces, glandular trichomes have become model structures to investigate the cellular biology of phytochemical production. In this review, we survey the structural and functional diversity of glandular trichomes across plant taxa, their roles in producing various classes of natural products, the major biosynthetic pathways housed in these "mini-factories" and the genetic regulation of their development and metabolic output. We also discuss modern techniques used to study glandular trichomes and highlight applications in biotechnology and medicinal plant improvement.

2. STRUCTURAL AND FUNCTIONAL DIVERSITY OF GLANDULAR TRICHOMES

Glandular trichomes are multicellular secretory structures that arise from protodermal (epidermal) cells and exhibit remarkable diversity in form, size, and distribution on plant organs (Muravnik, 2020). They vary from tiny capitate trichomes with a single-celled glandular head to larger peltate trichomes with a multicellular head, often on a short stalk. Capitate trichomes typically consist of a basal cell, a stalk cell, and a single secretory head cell, whereas peltate trichomes have a broader head of many secretory cells sitting on one or two stalk cells (Jing et al., 2014; Muravnik, 2020).

Individual plants often bear multiple trichome types – for example, tomato (*Solanum lycopersicum*) has eight distinct trichome forms (four glandular and four non-glandular) on its stems and leaves (Flood, 2019). The density and placement of glandular trichomes can vary by species and organ, reflecting adaptive strategies.

Functionally, glandular trichomes serve as combined structural and chemical defense units for plants. They act as physical barriers (hairs that impede insect movement or create a boundary layer on the leaf) and as sites of concentrated chemical release, often deterring pests upon contact (Bergau et al., 2015). Many trichomes secrete sticky or noxious substances that can trap, repel, or poison herbivorous insects. At the extreme, carnivorous plants like sundews (genus *Drosera*) have evolved glandular trichomes that exude mucilaginous enzymes to capture and digest insects (Bergau et al., 2015; Flood, 2019). More commonly, however, the secretions are defensive or protective: for instance, glandular hairs on *Urtica dioica* (stinging nettle) inject irritants as a deterrent (though these are technically cystolithic trichomes), and those on *Tithonia* and *Solanum* species exude insecticidal resins. Trichome secretions also protect against

microbial pathogens – many contain antifungal or antibacterial compounds that suppress infection on the plant surface. In addition to biotic defense, glandular trichomes help plants cope with abiotic stresses. They can secrete UV-absorbing flavonoids or other phenolics that form a chemical sunscreen, and their presence on the surface may reflect excess light and reduce leaf temperature or water loss. Indeed, the formation of glandular trichomes in different lineages is thought to be driven by the need to protect plants from herbivores, pathogens, intense light (UV-B), and heat (Muravnik, 2020).

Despite this functional diversity, a unifying feature of glandular trichomes is their extraordinary capacity to synthesize and accumulate specialized metabolites. These secretory cells are metabolically hyperactive, often producing and storing compounds at concentrations that would be cytotoxic elsewhere in the plant. To manage this, many glandular trichomes have evolved internal or external storage compartments. In some types, the secreted product is compartmentalized in a subcuticular storage cavity (a space between the cell wall and cuticle) – as seen in the large peltate glands of mint and cannabis, where a dome-like cuticle retains the essential oil or resin that the head cells produce. Storing the metabolites in an extracellular cavity prevents autotoxicity to the producing cells and allows accumulation of high concentrations (Tanney et al., 2021). Other trichomes continuously exude their products to the plant surface (forming a coating of exudate such as the sticky sugar esters on wild tobacco leaves) or sequester them in vacuoles within the trichome cells. From a structural standpoint, the secretion mechanism can thus differ: some glandular hairs release their contents only when the cuticle ruptures or when the trichome is mechanically damaged, whereas others slowly seep out products through microscopic pores or along the sides of the trichome. Additionally, glandular trichomes are often short-lived "expendable" organs – certain types secrete a burst of metabolites and then senesce or reload, corresponding to what Werker (1993) classified as "short-term" vs "long-term" glandular hairs based on secretion timing (short-term glands quickly unload a one-time secretion, whereas long-term glands can repeatedly secrete over time) (Ascensão et al., 1999; Muravnik, 2020). This dynamic aspect highlights that glandular trichomes are not static storage structures but actively metabolizing and sometimes transient organs. Overall, the structural variability (unicellular vs. multicellular, capitate vs. peltate, presence or absence of a storage cavity, etc.) underpins a wide range of functional roles across plant species.

3. ROLE IN PHYTOCHEMICAL BIOSYNTHESIS ACROSS DIFFERENT TAXA

Glandular trichomes are truly natural cell factories, responsible for much of the chemical diversity that plants produce for defense, signaling, and interaction with their environment. Across the plant kingdom, these glands have independently evolved in many lineages and often converged on similar functions. They are especially prominent in certain families – for example, the mint family (*Lamiaceae*) is characterized by abundant peltate glandular trichomes that produce essential oils, while the sunflower family (*Asteraceae*) often has capitate trichomes that secrete bitter terpenoids and other deterrents. In fact, some of the most famous plant natural products come from glandular trichomes: the antimalarial sesquiterpene lactone artemisinin is produced in the capitate trichomes of *Artemisia annua* (wormwood), and the psychoactive

cannabinoids (THC, CBD) of Cannabis sativa are synthesized in stalked glandular trichomes on the female flowers (Chang et al., 2024). These examples underscore how trichomes act as biofactories for important pharmaceuticals and bioactive compounds.

Notably, multiple classes of phytochemicals are made in trichomes, and a single plant may deploy trichomes to produce different compounds in different organs. For instance, *Solanum* species (nightshades) have glandular trichomes that exude acylsugars (sugar esters) as a sticky insect trap on leaves, while other trichomes on the same plant emit volatile terpenes that repel pests. In wild tomatoes (*Solanum habrochaites*, *S. pennellii*), high densities of type IV and VI glandular trichomes correlate with increased insect resistance due to the cocktail of acylsugars and terpenoids they secrete. By contrast, the cultivated tomato has fewer glandular trichomes and correspondingly lower levels of these defensive chemicals, illustrating how domestication can reduce natural chemical defenses (Huchelman et al., 2017).

Across different taxa, glandular trichomes often fulfill ecological roles such as: (i) Herbivore Defense – deterring feeding or oviposition by insects via toxic or antifeedant metabolites (e.g. nicotine and related alkaloids in tobacco can exude onto leaf surfaces, and numerous terpenes produced by trichomes deter herbivory) (Glas et al., 2012); (ii) Pathogen Defense – secreting antimicrobial agents (e.g. thymol and carvacrol in thyme trichomes are strongly antifungal); (iii) Attraction of Pollinators or Mutualists – in some plants, glandular trichomes produce floral oils or scents that attract pollinators or predators of herbivores. For example, species of *Dalechampia* and *Calceolaria* have glandular hairs on flowers that secrete oils collected by specialized bees, and some carnivorous plants use sweet exudates from trichomes to lure prey. Thus, while defense is a primary role, trichome metabolites can also mediate beneficial interactions.

Importantly, glandular trichomes are often metabolically specialized for certain compound classes within a given species. This means a particular trichome type usually produces a limited set of related compounds in very high amounts (Huchelman et al., 2017). This specialization is evident in the chemical profiles across taxa: Lamiaceae trichomes predominantly make monoterpenes and other volatile terpenoids (which give culinary herbs like basil, oregano, and mint their aroma), Asteraceae trichomes often produce sesquiterpene lactones and other bitter compounds (contributing to the medicinal bitterness of chamomile, feverfew, etc.), and *Solanaceae* trichomes may generate phenylpropanoid derivatives, acylsugars, or methylketones as defense chemicals (Huchelman et al., 2017). Even alkaloids – a class more commonly associated with internal secretory cells – can be found in glandular trichomes of some taxa. For instance, a histochemical study of thyme (Thymus) detected alkaloids localized specifically in both capitate and peltate trichome cells (staining positive with Dragendorff's reagent) while the rest of the leaf tissue was free of alkaloids (Jing et al., 2014). This indicates that alkaloid biosynthesis or accumulation in those species is compartmentalized in the trichomes. In tobacco (*Nicotiana*), certain nicotine-related alkaloids and diterpenes (like cembranoids) are present in trichome exudates, contributing to the plant's sticky defensive coating.

In summary, throughout the plant kingdom glandular trichomes are repeatedly used as sites of high-yield production of specialized metabolites crucial for survival. Some genera (e.g. Mentha, Lavandula, Cannabis) have been effectively "domesticated" for their trichome products –

peppermint oil, lavender oil, or cannabis resins – emphasizing the value of these structures. Glandular trichomes, though varied in morphology across taxa, universally function as micro-chemical reactors that enhance plant fitness by deploying chemical defenses and other ecologically relevant compounds on the plant's exterior.

4. MAJOR BIOSYNTHETIC PATHWAYS IN GLANDULAR TRICHOMES

Glandular trichomes are biochemically versatile, capable of synthesizing compounds from all major classes of plant secondary metabolites. Key pathways for terpenoids, phenolics, and alkaloids (among others) are often highly active in trichome cells, sometimes in a unique or modified form compared to the same pathways in other tissues. A remarkable feature is that trichomes tend to channel metabolic flux into a narrow set of end-products (the compounds that define that plant's chemical profile) in extraordinary quantities (Huchelman et al., 2017). Below we provide an overview of the major phytochemical classes produced in glandular trichomes and the biosynthetic routes involved, noting that these pathways frequently intersect with primary metabolism and are tightly regulated within the trichome.

4.1. TERPENOIDS

Terpenes and terpenoids (isoprenoids) are arguably the most common class of compounds in glandular trichomes. These include monoterpenes (C_10), sesquiterpenes (C_15), and diterpenes (C_20), which often constitute essential oils, resins, and gums. In trichomes of many aromatic plants (mint, basil, sage, etc.), monoterpenes like menthol, limonene, and pinene are synthesized via the plastid-localized MEP (methylerythritol phosphate) pathway, whereas sesquiterpenes like patchoulol or artemisinin derive from the cytosolic mevalonate (MVA) pathway – though cross-talk between the two pathways can occur. For example, studies in snapdragon flowers showed that the plastidial MEP pathway was supplying precursors for both monoterpene and sesquiterpene biosynthesis in glandular cells (Huchelman et al., 2017), highlighting the metabolic flexibility of trichomes. The typical terpenoid biosynthetic machinery in trichomes includes terpene synthase enzymes (e.g., menthone synthase in peppermint trichomes; amorpha-4,11-diene synthase in Artemisia gland cells) that convert universal C_5 building blocks (IPP/DMAPP) into cyclic or acyclic terpene skeletons, often followed by cytochrome P450 monooxygenases and specialized transferases to produce oxidized, polyoxygenated terpenoids. Trichome cells are often enriched in organelles needed for terpene biosynthesis: they harbor abundant leucoplasts (plastids without pigments) for monoterpene synthesis and well-developed smooth endoplasmic reticulum for sesquiterpenes and diterpenes that require P450s (Muravnik et al., 2020). Notable examples of terpenoids from trichomes include the essential oils of herbs (rich in mono- and sesquiterpenes), the glandular resins of conifers and Cannabis (rich in diterpenoid and terpenophenolic resins), and defensive terpenes in tomato (e.g. zingiberene and α-tomatine in wild tomato type VI trichomes). The yields are impressive – some peppermint cultivars exude >1% of leaf dry weight as monoterpene oil from trichomes. Because terpenoids are volatile or semi-volatile, they often

evaporate or diffuse from trichomes, forming a chemical plume that deters insects or attracts pollinators, depending on context.

4.2. PHENOLICS AND PHENYLPROPANOIDS

Glandular trichomes of many species produce compounds derived from the phenylpropanoid pathway, which transforms phenylalanine into a variety of aromatic metabolites. These include simple phenylpropanoids (such as eugenol, chavicol, etc.), flavonoids, and related polyphenols. In basil (*Ocimum basilicum*), for instance, peltate trichomes accumulate phenylpropanoid aroma compounds like chavicol and methyl eugenol in addition to terpenes (Huchelman et al., 2017; Türkay et al., 2023; Türkay et al., 2024). Some trichomes secrete flavonoid aglycones or flavonoid glycosides onto the surface; these can act as UV protectants or antimicrobial agents. Glandular trichomes of Teucrium species secrete sticky flavonoids that form a crust on the leaf. The enzymes of phenolic biosynthesis (e.g., phenylalanine ammonia-lyase (PAL), cinnamate 4-hydroxylase, and various reductases and transferases) have been found to be highly expressed in trichome cells of phenolic-rich plants (Huchelman et al., 2017). In some cases, the phenolics from trichomes contribute to plant taste and pigmentation – e.g., *Cannabis* trichomes produce not only cannabinoids but also flavonoids that can color the resin; *Pelargonium* glandular hairs secrete quercetin derivatives that end up on the leaf surface. An important subset of phenolics in trichomes are the phenylpropanoid volatiles (like vanillin, isoeugenol) that add to floral or leaf scents. These often arise from the shikimate/phenylpropanoid pathway and might be formed in concert with terpenes. In basil, coordinated regulation of phenylpropanoid and terpenoid synthesis in trichomes has been observed, indicating these pathways can be co-activated to produce a particular blend of metabolites (Huchelman et al., 2017).

4.3. ALKALOIDS

While many plant alkaloids are made in internal tissues (e.g. roots or phloem) and stored in vacuoles, there are cases where glandular trichomes participate in alkaloid biosynthesis or secretion. The pyridine alkaloid nicotine, for instance, is synthesized in tobacco roots but it can be transported to leaf trichomes and concentrated in trichome exudate along with sugary compounds – forming a toxic mix on the leaf surface of *Nicotiana*. Certain tropane alkaloids (like scopolamine) in genus *Datura* have been suggested to effuse from young stem trichomes. Direct evidence comes from histochemical studies: in Thymus species, glandular trichomes tested positive for alkaloids, indicating these cells either produce or accumulate alkaloidal compounds (Jing et al., 2014). Another example is the ergot alkaloids found on some grasses: an intriguing recent discovery showed endophytic fungi living in grass glandular trichomes produce ergot alkaloids on the surface (Steiner et al., 2015), effectively using the trichome as a delivery structure. In general, alkaloid presence in trichomes is less common than terpenes or phenolics, but when it occurs, it adds a potent layer of chemical defense (since many alkaloids are neurotoxic or feeding deterrents). As analytical techniques improve, new alkaloids localized to trichomes continue to be identified. The biosynthetic pathways for alkaloids in trichomes follow the same core enzymatic steps as elsewhere (e.g., decarboxylation of amino acids, BIA

pathway for benzylisoquinoline alkaloids, etc.), but often the final steps or regulation might be tailored to trichome expression. For instance, a atropa species might express a final O-methyltransferase for scopolamine predominantly in its trichomes if that's where the plant deploys the compound.

4.4. SPECIALIZED LIPIDS AND OTHERS

In addition to the classic categories above, glandular trichomes produce various unusual metabolites. Acyl sugars (sugar esters of fatty acids) are produced in high quantities by trichomes of wild tomatoes and some petunias as a sticky defense; these are synthesized by acyltransferases that are expressed almost exclusively in the glandular head cells. Methylketones (e.g., 2-tridecanone and 2-undecanone) are secreted by type VI trichomes of certain *Solanum* species; they derive from fatty acid pathways and have strong insecticidal activity (e.g., against whiteflies) (Huchelman et al., 2017). Cardenolides and other defensive steroids can also accumulate in trichome exudates in some *Apocynaceae* and *Solanaceae*. Essentially, if a plant benefits from having a defensive or communicative chemical at its surface, evolution often routes that compound's production into a glandular trichome. This partitioning is advantageous because the toxic or deterrent compound is confined to an expendable external cell, protecting the rest of the plant from harm while maximizing impact on the target (herbivore, microbe, etc.).

It is noteworthy that glandular trichomes often exhibit a degree of metabolic compartmentalization. Within a single trichome cell, different organelles handle different steps: plastids, cytosol, ER, vacuoles, and the apoplast may all be involved in a single compound's biosynthesis. For example, in *Cannabis* trichomes, cannabinoid biosynthesis starts in the cytosol (with phenolic precursors), continues in plastids (where the terpenoid moiety is made), and finishes in the apoplastic space of the secretory cavity where the two parts condense to form THCA, which then accumulates under the cuticle (Tanney et al., 2021). Such multi-step routing requires transporters or facilitators to shuttle intermediates between compartments. This level of metabolic orchestration is part of what makes glandular trichomes excellent model systems for studying the integration of biosynthetic pathways within a single cell type.

In summary, glandular trichomes are hotspots of secondary metabolism, adept at producing terpenoids, phenylpropanoids, alkaloids, and other specialized compounds. The major biosynthetic pathways operating in trichomes are the same core pathways found in plants at large, but in trichomes they are often upregulated and optimized to funnel precursors into a narrow set of outputs. This results in the accumulation of particular chemicals in amounts rarely seen in normal cells. Understanding these pathways in the trichome context has practical implications (as discussed later) for metabolic engineering and enhancing the production of high-value plant metabolites.

5. GENETIC AND MOLECULAR REGULATION OF PHYTOCHEMICAL PRODUCTION IN GLANDULAR TRICHOMES

The development of glandular trichomes and the regulation of their metabolic activity are tightly controlled by genetic networks. Research in recent years has begun to unravel the molecular players that specify where and how glandular trichomes form, as well as those that activate the biosynthetic pathways within trichome cells. This section discusses (a) the genetic control of glandular trichome development (how plants decide to make a glandular trichome and ensure it becomes a secretory cell type), and (b) the regulatory mechanisms that govern phytochemical biosynthesis in trichomes (transcription factors, signaling pathways, etc. that turn on the production of secondary metabolites).

5.1. DEVELOPMENTAL REGULATION OF GLANDULAR TRICHOMES

Plants use a combination of general and specialized regulators to initiate glandular trichomes. In the model plant Arabidopsis thaliana, trichome development (though non-glandular in this species) is controlled by a well-known network of transcription factors: an R2R3 MYB (GLABRA1), bHLH proteins (GL3/EGL3), and a WD40 repeat protein (TTG1) form a complex that activates trichome formation, while single-repeat MYBs (TRY/ CPC) act as inhibitors to create spacing patterns. In plants with multicellular glandular trichomes like tomato, tobacco, and Artemisia, homologous networks exist but with additional layers of regulation for the multicellular and glandular character. A key regulator in tomato is the *Woolly (Wo)* gene, which encodes an HD-ZIP IV transcription factor. Wo is essential for the formation of both glandular and non-glandular trichomes in tomato (and likely in many other species with multicellular trichomes). Mutations in Wo (such as the classical woolly mutant of tomato) result in a near hairless phenotype, whereas overexpression leads to excess trichome formation – indicating Wo has a dose-dependent, positive role in trichome initiation and development. Another crucial regulator in tomato is a basic helix–loop–helix (bHLH) transcription factor called SlMYC1. Recent studies showed that SlMYC1 is necessary for the development of the most abundant glandular trichomes (type VI) in tomato: CRISPR knockout lines completely lacked type VI trichomes (Xu et al., 2018). Interestingly, when SlMYC1 was knocked out, a novel aberrant trichome type appeared (termed type “VII-like”), suggesting that other factors initiate a prototrichome that fails to fully differentiate without SlMYC1 (Flood et al., 2019). This bHLH likely works in concert with MYB partners and hormonal signals (similar to how Arabidopsis GL3 works with GL1). Indeed, SlMYC1 is part of the jasmonate signaling pathway – as a JA-responsive bHLH, it connects herbivore stress signals to both trichome development and compound production.

Only a few trichome-specific regulators have been characterized so far, and the field is rapidly evolving. A breakthrough in 2024 identified two tomato genes, *Gland Cell Repressor 1* and *2* (*GCR1*, *GCR2*), which encode MYB-like transcription factors that act as negative regulators of glandular fate. These *GCR* genes are expressed in early developing trichomes and prevent excessive gland cell formation; when both are knocked out, tomato develops enlarged glandular trichomes (implying more secretory cells per trichome). Notably, homologs of *GCR* in tobacco and petunia appear to have a similar repressive role, suggesting a conserved mechanism across

species. The *GCR* repressors are part of a two-step regulatory process: they themselves are kept in check by an upstream repressor (in tomato, a *TOE1* homolog, part of the *AP2* miR172 pathway) that relieves inhibition at the right time. On the flip side, positive regulators like Leafless (LFS) in tomato have been proposed to promote gland formation, being the targets that *GCR* represses In tobacco, a MIXTA-like MYB transcription factor has been implicated in trichome formation on leaves (MIXTA is known in petunia for epidermal cell patterning and likely has parallels in trichome cell patterning) (Chang et al., 2024).

Hormonal regulation is another key aspect: jasmonic acid (JA) strongly induces glandular trichome development in many species. JA-deficient tomatoes have fewer trichomes and lower terpene production, while application of JA or its mimic can increase trichome numbers and chemical output. This effect is partly mediated by JA-responsive transcription factors such as SlMYC1 (which, as noted, is JA-inducible and necessary for trichome development). Conversely, gibberellins (GA) and other hormones can modulate trichome initiation in species-specific ways – e.g., applying GA to peppermint was found to increase trichome density and essential oil yield by upregulating biosynthetic genes (Huchelman et al., 2017). Cytokinin and auxin signaling have also been linked to trichome initiation in some studies, although JA is the dominant positive signal for glandular trichomes associated with defense. In summary, the developmental fate of a glandular trichome is determined by a network of transcription factors (MYB, bHLH, HD-Zip, etc.) operating under the influence of plant hormone signals and possibly small RNAs. Many of these regulators have dual roles, affecting both the physical development of the trichome and the activation of metabolic pathways within.

5.2. REGULATION OF PHYTOCHEMICAL PRODUCTION

Once a glandular trichome cell is formed, it must activate the suite of enzymes required to produce its specialized metabolites. This is achieved through trichome-specific or trichome-enhanced expression of biosynthetic genes, controlled by developmental and environmental cues. Often the same transcription factors that drive trichome development continue to upregulate secondary metabolism genes in those trichomes. A striking example is again *SlMYC1* in tomato: knockdown of *SlMYC1* (which allowed a few trichomes to still form) led to a drastic reduction in the expression of terpene synthase genes and a corresponding drop in monoterpene levels, even in plants that still had glandular trichomes present (Flood et al., 2019). This demonstrates that *SlMYC1* is required not only for making the trichome itself but also for turning on the terpenoid biosynthetic pathway within that trichome. Similarly, in Artemisia annua, a bHLH transcription factor (AaMYC2) and an AP2/ERF factor (AaERF1, also called ARTF1) have been identified that bind to promoters of artemisinin pathway genes (like *ADS*, *CYP71AV1*) and enhance their expression specifically in trichome cells, especially under JA stimulation. Other transcriptional activators such as WRKYs and MYBs (e.g., AaWRKY9 in *Artemisia*, or TcMYB2 in *Camellia* trichomes for tea catechins) have been found to orchestrate the production of particular compounds.

Frequently, these regulatory genes are part of inducible defense pathways. When a plant is attacked or stressed, signals like JA, salicylic acid, or abiotic stress signals can elevate the production of trichome chemicals. For instance, wounding or herbivory triggers a JA burst that

in tomato not only prompts more trichomes but also increases the output of terpenes and acylsugars from existing trichomes. Trichomes can even serve as "sensor" cells; tomato type VI trichomes store jasmonic acid (in its active form JA-Ile) and upon being touched or damaged by insects, they release it, thereby alerting the plant and systemically enhancing defense responses (Flood et al., 2019). This implies a feedback loop where trichome-produced JA can amplify its own biosynthetic pathways in a positive reinforcement cycle.

On the genomic level, plants often cluster genes for particular trichome-produced metabolites. For example, in some wild tomatoes, the genes encoding enzymes for acylsugar biosynthesis are physically grouped in the genome, allowing coordinated regulation. A notable case is a cluster of several methylketone synthesis genes in *Solanum habrochaites* (discovered to underlie insect resistance); by introgressing this cluster into cultivated tomato, researchers enhanced glandular methylketone output and pest resistance (Huchelman et al., 2017). Such gene clusters likely share regulatory sequences that trichome-specific transcription factors recognize. Comparative genomics has revealed that related species often have conserved blocks of trichome metabolism genes – for example, *Nicotiana* and *Solanum* (both Solanaceae) have some syntenic regions for trichome diterpene biosynthesis, hinting at an evolutionary conservation of regulatory modules.

Apart from transcription factors, post-transcriptional and enzymatic regulation also fine-tune phytochemical production. Glandular trichomes express specific microRNAs and RNA-binding proteins that can modulate the stability of mRNAs for pathway enzymes (this area is still being explored). At the enzyme level, the compartmentalization we discussed means that transporters and enzyme allostery play roles. Trichomes express unique transport proteins to move metabolites or precursors: for instance, an ABC transporter in petunia (PhABCG1) exports volatile phenylpropanoids from cells, and in tobacco a glandular-specific lipid transfer protein (NtLTP1) is required for secretion of hydrophobic diterpenes to the outside (Huchelman et al., 2017). Disrupting these transport processes can cause accumulation of products in the wrong place or feedback inhibition of the pathway. Thus, the molecular regulation of trichome biosynthesis includes not just turning genes on, but also ensuring their products are efficiently moved and stored.

In summary, the genetic and molecular regulation of glandular trichomes operates on two synergistic fronts: morphogenesis (driven by a network of developmental genes influenced by hormones) and metabolic pathway activation (driven by both the developmental network and by specialized metabolic regulators). Only a handful of master regulators (like Wo, SlMYC1, AaMYC2, etc.) have been characterized to date, and current research continues to identify new ones (e.g., the *GCR* repressors) (Chang et al., 2024). A deeper understanding of these regulatory circuits is not only of fundamental interest (elucidating how a plant cell differentiates into a high-output producer of secondary metabolites), but also of practical value for engineering plants with enhanced natural product output.

6. METHODS AND TECHNIQUES FOR STUDYING GLANDULAR TRICHOMES

Investigating glandular trichomes requires an integrated approach, as one must examine both their structural traits and their complex chemistry. Fortunately, because trichomes are external and often abundant, they are amenable to a variety of microscopy, molecular, and analytical techniques. Here we outline key methods used in glandular trichome research, ranging from visualization of trichome anatomy to omics technologies for profiling their genes and metabolites.

6.1. MICROSCOPY AND IMAGING

Microscopy is fundamental for characterizing trichome morphology and development. Light microscopy (bright-field or differential interference contrast) is used to observe trichome form on plant surfaces and in section. For example, simple visual examination under light microscopy distinguishes capitate vs peltate trichomes and can reveal contents (e.g., refractive droplets of oil in a gland head). Histochemical staining techniques can localize classes of chemicals in situ – as demonstrated by Dragendorff's reagent staining of alkaloids in *Thymus* trichomes, producing an orange color specifically in the secretory cells (Jing et al., 2014). Fluorescence microscopy and confocal laser scanning microscopy are used to probe trichome cellular structure; many glandular metabolites (like chlorogenic acid or flavonoids) are autofluorescent and can indicate distribution within the trichome. Researchers also use fluorescent dyes to test membrane integrity or the presence of cuticular holes in glands. For surface architecture, scanning electron microscopy (SEM) provides high-resolution images of trichome shape, density, and the presence of subcuticular spaces or pores. SEM has been extensively used to survey trichome types on new plant species and to monitor trichome development (e.g., capturing images of a developing multicellular trichome at different stages). Transmission electron microscopy (TEM) goes further to visualize ultrastructure: it can show the dense cytoplasm of secretory head cells, the enlarged plastids filled with lipid vesicles (terpenoid precursors), abundant smooth ER, and the cuticle layer bulging to form a storage cavity (Tanney et al., 2021). TEM also allows observation of the mode of secretion – for instance, vesicles fusing with the plasma membrane to release contents into the cell wall space. Newer imaging methods like 3D electron tomography and atomic force microscopy have also been applied to special cases (e.g., mapping the thickness of the cuticle over a gland or the turgor pressure within a secretory cell).

6.2. TRICHOME ISOLATION AND CELL-SPECIFIC ANALYSIS

A major advantage in trichome research is that trichomes and their exudates can be harvested relatively easily from the plant surface (Glas et al., 2012). This allows scientists to study trichome chemistry and genetics in relative isolation from the rest of the leaf. Methods for isolating trichomes include mechanical brushing or shaving of leaves (to physically remove the trichomes), solvent washing (a quick dip in solvent can strip off surface exudates or even knock off trichome glands), and more refined techniques like laser capture microdissection (LCM). In LCM, microscopic laser cuts can excise individual glandular trichome cells from tissue sections

for downstream RNA or metabolite analysis – this has been used in plants like Medicago to profile trichome-specific gene expression. Another innovative approach is flow cytometry for trichome cells: researchers have exploited natural autofluorescence of glandular trichome cells (due to their rich metabolites) to separate them. For example, Bergau et al. (2015) dissociated tomato leaf cells and used fluorescence-activated cell sorting (FACS) to collect developing trichome cells, enabling transcriptomic analysis of trichomes at different maturation stages (Huchelman et al., 2017). Additionally, density gradient centrifugation can pellet trichomes from a leaf homogenate (since trichomes often have distinct size/density). Once isolated, trichome-rich preparations can be subjected to omics analyses (detailed below) or biochemical assays. It is also possible to isolate the exuded compounds specifically – for instance, by gentle rinsing of the leaf with solvent or by using tiny capillaries to sample the droplets under the trichome cuticle in species like *Cannabis*. The ease of trichome/exudate collection has been a boon: it has "permitted a detailed study of their metabolites, as well as the genes and proteins responsible for them" (Glas et al., 2012), essentially allowing researchers to link chemistry with gene expression in the same cell type.

6.3. OMICS TECHNOLOGIES (TRANSCRIPTOMICS, PROTEOMICS, METABOLOMICS)

Modern high-throughput methods have revolutionized the study of glandular trichomes. Transcriptomic profiling (RNA-seq) of isolated trichomes or trichome cells identifies which genes are highly expressed relative to non-trichome tissue. Such studies have uncovered transcripts for all enzymes of certain pathways, confirming that (for example) mint peltate gland cells contain the full suite of monoterpene biosynthetic genes, or that in Lavandula, genes for both terpene and phenolic synthesis are co-expressed in glands. A comparative trichome transcriptome analysis in different mint species helped explain differential menthol production by correlating gene expression levels of key pathway enzymes. There are now trichome transcriptome datasets for many species, compiled in resources like the TrichOME database (a comparative omics database for plant trichomes). This database allows researchers to query genes of interest across multiple trichome transcriptomes to find common regulators or enzymes. On the protein side, proteomic analyses of trichomes have been attempted, though obtaining sufficient material is challenging. In one case, Champagne and Boutry (2013) performed proteomics on glandular trichomes of a non-model plant, identifying many abundant enzymes and unique proteins in the trichome cells. Proteomics can reveal, for instance, specialized isoforms of enzymes or abundant carrier proteins (like the aforementioned lipid transfer protein in tobacco trichomes). Metabolomics is, of course, central – using GC-MS, LC-MS, NMR, and other analytical chemistry techniques to profile the compounds present in trichomes. Coupling metabolomic data with transcript profiles helps assign functions to genes (e.g., if a certain unknown cytochrome P450 is highly expressed in trichomes at the same time a unique compound appears, it hints that the P450 may be responsible for that compound's synthesis). A comprehensive approach is exemplified by a multi-omics study on tomato glandular trichomes. Balcke et al. (2017) integrated transcriptomics, proteomics, and metabolite analysis and found that tomato glandular trichomes have distinct central metabolism geared towards producing large amounts of sucrose and amino acids to support rapid specialized

metabolite synthesis. This kind of systems biology approach can identify bottlenecks in pathways or unusual metabolic adaptations in trichomes (for example, an upregulation of glycolysis to provide extra acetyl-CoA for terpenoid biosynthesis) (Huchelman et al., 2017).

6.4. GENETIC AND GENOMIC APPROACHES

To understand gene function in trichome development and metabolism, researchers employ genetic approaches such as mutants, transgenics, and gene editing. Classical mutant screening has identified numerous "hairless" or "excess hair" mutants in plants like *Arabidopsis*, tomato, cucumber, and others – these often correspond to key regulators (e.g., hairless in tomato is an allele of *Woolly*). Modern CRISPR-Cas9 gene editing has allowed targeted knockout of suspected trichome genes (for instance, knocking out candidate transcription factors like SlMYC1 (Flood et al., 2019) or metabolic genes to test their role in trichomes). Coupled with trichome-specific phenotypic assays (like measuring metabolite changes or trichome counts in the edited lines), this yields functional validation. Virus-induced gene silencing (VIGS) is another tool used particularly in species that are not easy to transform; VIGS in *Nicotiana* has been used to transiently silence genes in trichomes (for example, silencing a terpene synthase to see if a particular compound disappears from the exudate). On the flip side, overexpression of genes (often using trichome-specific promoters to target expression to trichomes) can be used to enhance certain pathways or trichome development. For instance, overexpressing a positive regulator like Wo or SlMYC1 in tomato results in a higher density of glandular trichomes and elevated levels of their metabolites (Chang et al., 2024). The availability of reference genomes for plants with glandular trichomes (e.g., the tomato genome, the tobacco genome, the cannabis genome, etc.) has accelerated discovery of gene candidates by enabling QTL mapping and genome-wide association studies for trichome traits. If a particular wild species has an exceptionally high metabolite from trichomes, crossing it with a low-producing line and doing QTL analysis can pinpoint genetic loci underlying the difference. This strategy was used with wild tomato species, leading to the identification of loci controlling acylsugar production and trichome density, which turned out to be clusters of metabolic genes (Huchelman et al., 2017).

6.5. ANALYTICAL CHEMISTRY AND FUNCTIONAL ASSAYS

Finally, specialized analytical techniques are employed to link structure with function. Gas chromatography-mass spectrometry (GC-MS) is the workhorse for volatile compounds: by enclosing a single leaf or even an intact plant in a chamber, one can sample the headspace to analyze trichome-emitted volatiles. Alternatively, individual trichomes or isolated exudate can be directly analyzed – for example, a single cannabis trichome's contents can be laser-desorbed and sent into a mass spectrometer (techniques like LDI-MS imaging). Liquid chromatography (HPLC/UPLC) helps quantify non-volatile, often more polar trichome compounds (like cannabinoids, glycosides, alkaloids). In the alkaloid-storing thyme trichomes mentioned, GC-MS of leaf extracts confirmed the presence of specific alkaloids in young leaves, correlating with the histochemical stain (Jing et al., 2014). To complement chemical analysis, bioassays are used to test the function of trichome metabolites. For instance, insect feeding trials on plant

lines with different trichome profiles can demonstrate that higher terpene or acylsugar levels (due to a genetic modification) confer greater pest resistance (Huchelman et al., 2017). Microbial growth assays with trichome exudates can show antimicrobial efficacy. Even simple assays like observing whether an insect avoids walking on a leaf with sticky trichomes provide functional insight.

In combination, these methodologies enable researchers to dissect glandular trichomes from the macro scale (distribution on the plant, ecological effects) down to the molecular scale (gene expression networks and enzyme functions). Glandular trichomes have thus become a model for single-cell type analysis in plants – akin to a "plant cell in a test tube" that can be studied in isolation. As new techniques emerge (such as single-cell RNA sequencing, or improved in vivo imaging), our ability to probe the inner workings of glandular trichomes will continue to grow, providing even deeper understanding of how these tiny biochemical factories operate.

7. APPLICATIONS IN PLANT BIOTECHNOLOGY, METABOLIC ENGINEERING, AND PHARMACEUTICAL RESEARCH

The unique properties of glandular trichomes – their capacity for high-level biosynthesis and secretion of valuable natural products – make them attractive targets for biotechnological applications. Harnessing trichomes can lead to crops with improved pest resistance, higher yields of commercially important phytochemicals, and even novel biofactories for drug production. Here we discuss how insights from trichome biology are being applied in agriculture and industry, and the future prospects for engineering these natural factories.

Enhancing Crop Protection: One major application is breeding or engineering crops with higher glandular trichome density or potency to naturally resist pests. Since glandular trichomes are often the first line of chemical defense, increasing their number or the amount of toxin they produce can reduce reliance on pesticides. For example, wild tomato species with dense, sticky trichomes are resistant to whiteflies and aphids, and breeders have introgressed these traits into cultivated tomato. A specific success story involved transferring a sesquiterpene biosynthetic pathway from a wild tomato (*Solanum habrochaites*) into cultivated tomato, which conferred strong resistance to insect herbivores (Huchelman et al., 2017). This was achieved by crossing (and, in modern approaches, by transgenic insertion) of the gene cluster responsible for producing the insect-repellent terpene zingiberene; the resulting plants accumulate the sesquiterpene in their glandular trichomes and are less damaged by pests. Similarly, breeding programs in crops like *Brassica* (mustard greens) and Solanum tuberosum (potato) are exploring wild relatives with more effective trichomes to introduce into elite varieties. In ornamental plants such as chrysanthemums, increasing trichome-borne pyrethrins (natural insecticides) is of interest.

Transgenic approaches have also been demonstrated: overexpressing trichome development regulators can amplify defense. In tomato, simultaneous overexpression of the *HD-Zip* gene Wo and the bHLH SlMYC1 (the "woolly/SlMYC1 module") led to a plant with a carpet of glandular trichomes that produced heightened levels of defensive compounds, significantly improving resistance to insects (Chang et al., 2024). This kind of genetic engineering essentially

turns up the dial on the plant's innate defense factory. Another approach is to engineer the biochemistry of trichomes: for instance, making the trichomes produce a new deterrent compound. A proof-of-concept was shown in tobacco, where researchers engineered trichomes to produce oxime-based volatiles that repel insects, by inserting a *CYP79* gene from maize under a trichome-specific promoter. The transformed tobacco emitted the volatile and showed reduced herbivory. Because trichomes localize toxic compounds away from vital tissues, plants can potentially tolerate higher levels of these bio-pesticides when they are trichome-targeted.

7.1. METABOLIC ENGINEERING FOR HIGH-VALUE COMPOUNDS

Glandular trichomes are often the sites of biosynthesis for plant-derived medicinal compounds. Thus, they present an opportunity for metabolic engineering to boost the supply of these pharmaceuticals. A prominent example is artemisinin from A. annua trichomes – efforts have been made to increase artemisinin yield by genetic means, such as overexpressing key enzymes (ADS, DBR2) or regulatory genes (the *AP2* factor *AaORA*) in the trichomes. Some success has been seen in doubling artemisinin content by transgenic approaches, although industrial production has also turned to synthetic biology in yeast. In *Cannabis*, where cannabinoids (THCA, CBDA) are made exclusively in glandular trichomes, there is intense interest in both classical breeding and biotech to increase cannabinoid yield or tailor the cannabinoid profile for medical applications. Understanding the gene network in cannabis trichomes (which genes control cannabinoid synthase expression, etc.) is guiding breeding for higher THC or CBD strains (Tanney et al., 2021). On the metabolic engineering front, one could foresee inserting the cannabinoid pathway into trichomes of a more easily grown plant or even engineering microbial systems with key elements from trichomes.

Transgenic metabolic engineering in trichomes has been demonstrated in model systems like tobacco – often referred to as a "trichome biofactory" for proof-of-concept. For instance, the production of taxadiene (a precursor of the anti-cancer drug Taxol normally from yew tree bark) was achieved in cultured tobacco cells by introducing a taxadiene synthase (Huchelman et al., 2017). While that was in cell culture, a similar idea is to engineer tobacco plants so that taxadiene accumulates in their glandular trichomes (tobacco trichomes can accumulate diterpenes, so they are a plausible surrogate host). As another example, transgenic mint plants were created to overexpress a cytochrome P450 and reductase, resulting in diversion of the monoterpene pathway to produce a novel compound in the peltate glands (demonstrating that one can reprogram the product profile of trichomes). The choice of promoter is crucial in such efforts; typically trichome-specific promoters (like the promoter of a trichome resin protein or a terpene synthase gene that is only active in gland cells) are used so that the transgene is expressed predominantly in the trichomes. This avoids burdening the rest of the plant with the metabolic perturbation and concentrates the effects in the trichome "factory." Additionally, engineering strategies often try to boost precursor supply for the target pathway: for terpenoids, this might mean upregulating the MEP pathway genes or diverting metabolic flux from primary isoprenoids into specialized terpenes. One study highlighted the importance of drawing from the existing metabolic pools – e.g. sinking more geranyl diphosphate into monoterpenes by

overexpressing a sink enzyme – and understanding the cross-talk between pathways to avoid bottlenecks (Huchelman et al., 2017).

7.2. COMMERCIAL CULTIVATION AND BIOPRODUCT HARVESTING

Beyond genetic engineering, knowledge of trichomes influences agricultural practices. For crops like mint, basil, lavender, and cannabis, growers aim to maximize glandular trichome formation because that directly translates to product yield (essential oil content or cannabinoid content). Horticultural research has shown that certain light spectra or mild stress can induce more trichomes. For instance, UV-B exposure can trigger higher flavonoid accumulation in trichomes as a protective response, so some growers use UV supplementation to enhance output. Similarly, moderate drought or nutrient stress at the right growth stage sometimes increases essential oil concentration by stimulating trichome development. However, these need to be applied carefully to avoid overall crop loss. In cannabis, where a multi-billion dollar industry relies on trichome-produced resin, there is interest in trichome-focused cultivation techniques and even mechanical or chemical elicitors that encourage trichome proliferation (Tanney et al., 2021). One could imagine foliar sprays of jasmonate or other elicitors to temporarily boost trichome density and metabolite production shortly before harvest – indeed, methyl jasmonate treatments have been used in artemisinin production fields to increase yield.

From a pharmaceutical research perspective, glandular trichomes are a treasure trove of natural compounds. Many new lead compounds (antimicrobials, anti-cancer agents, etc.) are discovered by screening trichome exudates from diverse plant species. Because trichomes often produce unique chemistries (sometimes not found elsewhere in the plant), they broaden the chemical diversity available for drug screening. Researchers are exploring under-investigated plants that have interesting traditional uses – often these have prominent aromatic or sticky trichomes – to isolate novel bioactive constituents. Once a valuable compound is identified, trichome-targeted metabolic engineering can be employed to upscale its production. There is also interest in synthetic biology to mimic trichome systems: for example, reconstructing a plant pathway in yeast or *E. coli*. However, certain steps (especially those requiring compartmentalization or membrane-bound enzymes) are challenging to replicate in microbes. In such cases, enhancing the native plant's production via trichomes might be more practical.

7.3. ENVIRONMENTAL AND INDUSTRIAL IMPLICATIONS

By leveraging glandular trichomes, we can develop plants that are more self-reliant in defense (reducing pesticide use) and that yield higher quantities of natural products (reducing the need for chemical synthesis of those products). The essential oils industry, which was valued at over $18 billion in 2020 (Tanney et al., 2021), depends largely on plants with glandular trichomes (like mint, lavender, lemongrass, etc.). Improving trichome productivity in those crops has direct economic benefits. In some cases, breeding has unintentionally reduced trichome counts for aesthetic reasons (e.g., smoother leaves); biotechnology offers a way to reintroduce or amplify those traits without altering the plant's primary characteristics. Glandular trichomes have also been proposed as sites to produce non-native valuable compounds – for example,

engineering a fodder crop to produce an insect pheromone in its trichomes, turning the crop into a pest-confusing agent in the field.

In conclusion, glandular trichomes stand at the intersection of plant defense, natural product chemistry, and biotechnology. They exemplify how a single cell type can be programmed to perform extreme biochemical feats, and they offer a convenient target for scientific manipulation. Ongoing research is making it possible to dial the trichome's output up or down or even change its product mix. As our understanding deepens, we may see the development of "designer trichomes" – plants whose glandular hairs are custom-tailored to produce new compounds on demand. From more pest-resistant crops to sustainable production of medicines and fragrances, the potential applications of glandular trichome research are vast and impactful. Glandular trichomes, once merely an interesting microscopic feature, have now truly achieved "model status" as living laboratories for studying and engineering phytochemical biosynthesis (Chang et al., 2024).

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