

Review

The UGT73 Family of Glycosyltransferases in Plants: Gene Structure, Catalytic Mechanisms, and Biological Functions

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Abstract

Uridine diphosphate (UDP)-dependent glycosyltransferases (UGTs) play important roles in plant growth and development. As an important branch of plant UGTs, the UGT73 family participates in secondary metabolism, hormone regulation, and stress responses. Studies have shown that this family is involved in the synthesis of flavonoids, terpenoids, and other substances as well as the regulation of hormone homeostasis through precise glycosylation modifications. This review has collated the relevant properties of the plant UGT73 family in recent years and aimed to (1) analyze the structural characteristics of UGT73 family glycosyltransferase genes in different plant species; (2) outline the substrate specificity, catalytic sites, and mechanisms of UGT73 family glycosyltransferases; and (3) elaborate on their notable roles in growth and development, hormone regulation, and stress resistance. In-depth investigations are required to analyze the catalytic structure of the UGT73 family, complex regulatory networks, and interspecific functional differences. Future studies should combine multi-omic and synthetic biology technologies to explore new functions of the UGT73 family, thereby providing theoretical support and practical guidance for the development of plant metabolic engineering and green biotechnology.

Keywords: UGT73 family; glycosyltransferase; plant secondary metabolism; stress response; enzyme engineering; regulatory mechanism



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1. Introduction

During growth and development, plants produce various secondary metabolites that play crucial roles in processes, such as coping with biotic and abiotic stresses, signal transduction, and interactions with other organisms [1]. Glycosylation is a common yet important chemical modification method that is widely used in the synthesis and transformation of plant secondary metabolites. Glycosyltransferases (GTs) are the key enzymes that catalyze this modification reaction [2,3]. As of July 2025, the Carbohydrate-Active EnZymes Database (CAZy; <http://www.cazy.org>, access on 1 July 2025) classified GTs into 138 families and 1 unclassified family (GT-U) based on amino acid sequence similarity and three-dimensional structural characteristics [4]. Among all the GT families, GT family 1 is currently the largest and most widely distributed in plants, encompassing almost all the enzymes responsible for small-molecule glycosylation [5,6]. The GT family 1 includes a class

of enzymes represented by uridine diphosphate (UDP)-dependent glycosyltransferases (UGTs). These enzymes can catalyze the glycosylation reactions of various substrates and play key roles in numerous biological processes, such as plant secondary metabolite synthesis, hormone regulation, and environmental responses.

Plant UGTs are core members responsible for plant glycosylation [7]. UGTs can utilize UDP-sugars (such as UDP-glucose, UDP-galactose, UDP-arabinose, UDP-rhamnose, UDP-xylose, or UDP-glucuronic acid) [8]. As activated glycosyl donors, these UDP-sugars are transferred to various small-molecule acceptors, including but not limited to flavonoids, phenolic acids, terpenoids, alkaloids, and plant hormones. This process further alters the biological activity, solubility, stability, and transport properties of substrates, thereby playing a key role in plant growth and development, signal transduction, environmental adaptation, and interactions with external organisms [9]. For example, UGTs are involved in the glycosylation of flavonoids, terpenoids, alkaloids, and other substances, altering the polarity, stability, and biological activity of these compounds, thereby affecting plant flower color, aroma, taste, and defense capabilities [10–12]. In hormone regulation, UGTs can modulate the activity and homeostasis of plant hormones, such as IAA, cytokinins, and ABA. They convert hormones into inactive storage forms or regulate their subcellular localization through glycosylation, thereby regulating plant growth processes and developmental patterns [13,14]. Furthermore, plant UGTs play a pivotal role in the response to biotic (such as diseases and pests) and abiotic stresses (such as drought, high temperature, and salinity). For example, *PpUGT74F2* is inhibited by *Monilinia fructicola* in peaches (*Prunus persica*), and enhances disease resistance by reducing SA glycosylation to accumulate resistance signals [15]. In tea plants (*Camellia sinensis*), UGT89AC1 is induced by *Ectropis obliqua* and catalyzes the synthesis of quercetin-3-O-glucoside, thereby inhibiting larval feeding [12]. In alfalfa (*Medicago sativa*), *MsUGT003* and *MsUGT024* are upregulated under drought and ABA treatments. It has been speculated that they enhance drought tolerance by regulating metabolite glycosylation [16]. In maize (*Zea mays*), *ZmUGT92A1* positively regulates heat tolerance by maintaining flavonoid homeostasis and reactive oxygen species (ROS) balance [17]. Additionally, UGTs can also enhance the detoxification ability and stress resistance of plants by catalyzing the glycosylation of exogenous substances and toxic metabolites [18,19].

The UGT family is divided into 18 subgroups (A–R) in angiosperms. Members of subgroup D, specifically the UGT73 family, are widely distributed in various plants, such as the model plant *Arabidopsis thaliana* [20,21], tobacco (*Nicotiana tabacum*) [22], tea plants [23], licorice (*Glycyrrhiza uralensis*) [24], ginseng (*Panax ginseng*) [25], and other cash crops. With the rapid development of high-throughput sequencing technology and continuous accumulation of plant genome data, more UGT73 family members have been identified. Their quantities vary significantly among different plant species, which not only reflects the adaptive differentiation of the family during plant evolution but also provides an evolutionary perspective for analyzing its functional diversity. Studies have shown that UGT73 family members are involved in plant flavonoid, terpenoid, and phenolic acid metabolism through specific glycosylation modifications and play a key role in plant pigment formation, flavor substance accumulation, and medicinal ingredient synthesis. They can also regulate hormone activity and signal transduction by modifying plant hormones, such as IAA and ABA, thereby affecting plant growth and development processes, as well as stress responses. In addition, when plants respond to external stressors, the UGT73 family reduces the toxicity of toxins and harmful substances by catalyzing glycosylation, thereby enhancing plant stress resistance [26,27].

Despite considerable advances in UGT73 research, critical knowledge gaps remain regarding substrate specificity, catalytic mechanisms, regulatory networks, and post-

translational modifications. Deeper investigation of UGT73s is essential to elucidate their roles in plant secondary metabolism and stress adaptation and offers valuable targets for synthetic biology approaches aimed at improving crop quality, enhancing medicinal compound production, and developing stress-resistant varieties. This review summarizes current understanding of UGT73 family characteristics, functions, and applications, and suggests future research directions to advance the field.

2. Basic Characteristics and Evolutionary Features of Plant UGTs

According to the classification criteria of the International UGT Nomenclature Committee (<https://labs.wsu.edu/ugt>, access on 1 July 2025), UGTs are divided into families and subfamilies based on the similarity of their amino acid sequences. Based on multi-dimensional criteria, such as substrate specificity, amino acid sequence homology, and catalytic properties, UGT genes have been systematically classified into 106 families (GT1-GT106) [28]. The UGT gene nomenclature system followed a rigorous paradigm (Figure 1). The gene name uses “UGT” as the root symbol, followed by Arabic numerals indicating family affiliation, letters representing subfamily categories, and Arabic numerals designating individual genes in sequence, thereby endowing each UGT gene with a unique and clear identifier. Based on the nomenclature system, Families 1–50 mainly cover UGT genes of animal origin, Families 51–70 correspond to UGT genes from yeast, Families 71–100 belong to UGT genes of plant origin, which play a core regulatory role in the glycosylation modification of plant secondary metabolites, such as flavonoids and terpenoids and thus affect plant pigment synthesis, aroma formation, and the establishment of defense mechanisms, Families 101–200 are used to identify UGT genes from bacterial origin [29].

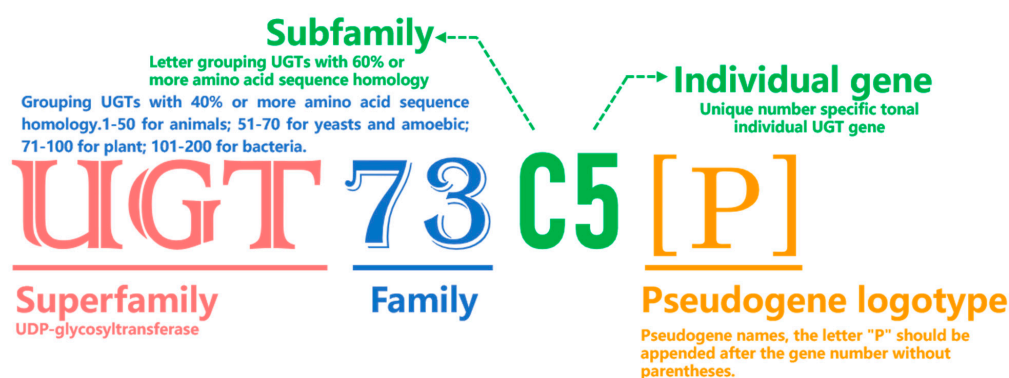


Figure 1. The Nomenclature Rules of UGT Genes. “UGT” denotes the superfamily, specifically the UDP-glycosyltransferase superfamily. “73” designates the family, which groups enzymes based on amino acid sequence homology; the numbering range for families varies across organisms, with plants, for example, ranging from family 71 to 100. “C” indicates the subfamily, assigned by grouping UGTs sharing 60% or higher amino acid sequence identity with a letter designation. “5” represents the individual gene, a unique identifier distinguishing specific genes within a subfamily. “[P]” is the pseudogene designation. The naming convention for pseudogenes appends the letter “P” (without brackets) directly to the gene number. The bracketed “[P]” form is used solely for illustrative purposes in diagrams/logos.

Researchers have conducted in-depth studies of numerous plant species and identified UGT gene family members in varying numbers. Relevant literature has elaborated the UGT genes identified in different plants and their specific quantities (Figure 2) [22,30–63]. Among lower plants, *Chlamydomonas reinhardtii* and *Chara braunii* have the smallest number of UGT genes, with only one and two identified UGT members, respectively [31]. This phenomenon is closely associated with their physiological requirements and evolutionary status: As structurally simple lower plants (the former being unicellular green algae, the latter multicellular charophytes but lacking true organ differentiation), their metabolic

networks are relatively rudimentary, primarily relying on basic photosynthetic metabolism and primary growth regulation. These organisms require only a limited number of UGTs to participate in core glycosylation processes (e.g., basic modifications of photosynthesis-related proteins or stability regulation of simple metabolites). Consequently, the UGT family has not undergone significant expansion. As plants evolved toward higher taxonomic groups—progressing from “embryo formation” (bryophytes, e.g., *Physcomitrella patens*, with approximately 15 UGT genes) to “organ differentiation” (pteridophytes), followed by “vascular tissue emergence” (gymnosperms, e.g., *Ginkgo biloba*, harboring approximately 129 UGT genes) [31], and ultimately to “seed/pollen production” (angiosperms, e.g., *Medicago sativa*, possessing up to 239 UGT genes) [59]—the number of UGT genes exhibited a stepwise increasing trend. This evolutionary shift represents a direct manifestation of plant adaptation to terrestrial environments and the increasing complexity of metabolic networks: the formation of embryos and organ differentiation drove the demand for hormonal regulation, with UGTs precisely orchestrating embryonic development and organogenesis through glycosylation of phytohormones, such as auxin and abscisic acid [64,65]; the emergence of vascular tissues enabled plants to achieve taller stature, where UGT-mediated glycosylation of cell wall polysaccharides (e.g., hemicellulose) and secondary metabolites (e.g., flavonoids, terpenoids) became pivotal for structural stability and stress resistance [13,66]; the development of seeds and pollen further refined reproductive processes, with UGTs enhancing reproductive success by glycosylating seed storage compounds (e.g., lipids, proteins) and pollen surface recognition molecules [64,67]. It is evident that the expansion of UGT gene family aligns closely with the evolutionary trajectory of plants characterized by “increasing structural complexity, metabolic diversification, and enhanced environmental adaptability,” serving as a crucial molecular hallmark of their transition from simple aquatic life forms to complex terrestrial higher plant lineages.

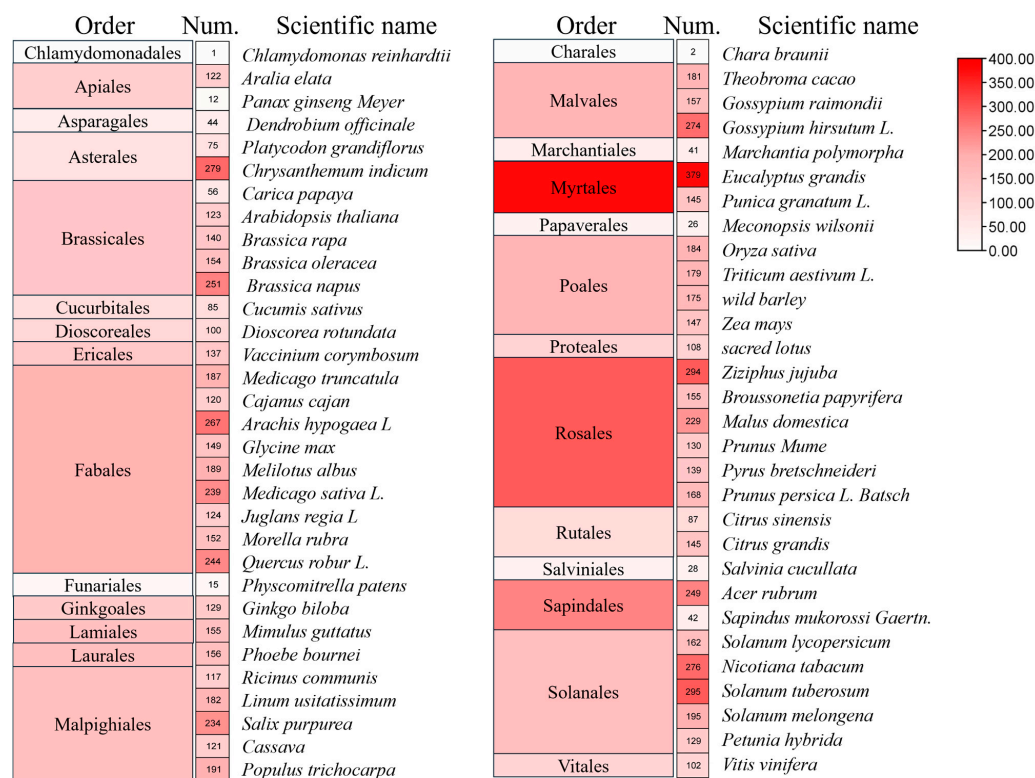


Figure 2. The number of UGTs in different plant species. Species included in the figure are listed in increasing order of their number *Chlamydomonas reinhardtii*, *Chara braunii*, *Panax ginseng* Meyer,

Physcomitrella patens, *Meconopsis wilsonii*, *Salvinia cucullata*, *Marchantia polymorpha*, *Sapindus mukorossi* Gaertn., *Dendrobium officinale*, *Carica papaya*, *Platycodon grandifloras*, *Cucumis sativus*, *Citrus sinensis*, *Dioscorea rotundata*, *Vitis vinifera*, *sacred lotus*, *Ricinus communis*, *Cajanus cajan*, *Cassava*, *Aralia elata*, *Arabidopsis thaliana*, *Juglans regia* L., *Ginkgo biloba*, *Petunia hybrida*, *Prunus Mume*, *Vaccinium corymbosum*, *Pyrus bretschneideri*, *Brassica rapa*, *Punica granatum* L., *Citrus grandis*, *Zea mays*, *Glycine max*, *Morella rubra*, *Brassica oleracea*, *Mimulus guttatus*, *Broussonetia papyrifera*, *Phoebe bournei*, *Gossypium raimondii*, *Solanum lycopersicum*, *Prunus persica* L. Batsch, *wild barley*, *Triticum aestivum* L., *Theobroma cacao*, *Linum usitatissimum*, *Oryza sativa*, *Medicago truncatula*, *Melilotus albus*, *Populus trichocarpa*, *Solanum melongena*, *Malus domestica*, *Salix purpurea*, *Medicago sativa* L., *Quercus robur* L., *Acer rubrum*, *Brassica napus*, *Arachis hypogaea* L., *Gossypium hirsutum* L., *Nicotiana tabacum*, *Chrysanthemum indicum*, *Ziziphus jujuba*, *Solanum tuberosum*, *Eucalyptus grandis*.

3. Characteristics and Functions of Group D UGTs in Plants

Within the phylogenetic framework of the plant UGTs superfamily, functional divergence among different family members leads to the formation of multiple distinct clades. Among these, groups A, B and E are well-recognized as major groups. Members of Group A play a central role in the regulation of plant secondary metabolism by participating in the glycosylation of flavonoids [68], Group B functions distinctly in glycosylation modifications associated with hormone signal transduction [69], and Group E is widely studied because of its close association with plant stress responses. The molecular mechanisms and physiological functions of these families are relatively well characterized [70]. Conversely, as another functionally diverse and evolutionarily conserved branch within this superfamily, Group D has not yet reached the same level of research depth as the aforementioned groups. Group D represents a functionally diverse and evolutionarily conserved branch, with its members widely distributed among angiosperms and exhibiting higher representation in monocots. Phylogenetically, the UGT73 family serves as the core lineage within Group D, alongside monocot-specific families, such as UGT98, UGT99, and UGT702. Gene duplication and functional divergence collectively enable Group D members to catalyze diverse substrates. The core function of Group D UGTs is to participate in the glycosylation of plant secondary metabolites. Its substrates include flavonoids, terpenoids and benzoates. Glycosylation predominantly targets hydroxyl groups (e.g., 7-OH), with UDP-glucose serving as the primary sugar donor, although some members utilize UDP-rhamnose or UDP-xylose [71]. For instance, *UGT706C2* from rice (*Oryza sativa*) catalyzes the glycosylation of the 7-OH group of flavonoids, such as apigenin and luteolin [72], whereas *UGT703H1* from the ornamental plant *Crocasmia crocosmiflora* functions as a 4-O-xylosyltransferase for flavonol glycosides and participates in the biosynthesis of the specialized metabolite montbretin A [73]. These functions underscore the pivotal role of Group D in plant environmental adaptation and bioactive compound accumulation. Glycosylation enhances compound stability, water solubility, or bioactivity. From the perspective of evolutionary dynamics, the expansion of Group D is closely linked to plant adaptation to complex environments. Tandem and large-scale duplication events drove the enlargement of this family, whereas purifying selection pressure maintained the stability of core catalytic domains, such as the conserved Plant Secondary Product Glycosyltransferase (PSPG) box [71]. Functional divergence among Group D members was achieved through refinement of substrate specificity. For instance, within the same subfamily, certain enzymes exclusively recognize flavonoids, whereas others preferentially act on terpenoids. This functional divergence provides an enzymatic basis for the diversity in plant secondary metabolism. Among all members of Group D UGTs, the UGT73 family is the most extensively studied and functionally characterized. Members of the UGT73 family are widely distributed across the plant kingdom and participate in the regulation of diverse critical biological processes.

Consequently, their functional diversity and evolutionary adaptability have become major focuses of UGT research.

4. Genomic Organization of Plant UGT73 Family Glycosyltransferases

UGT73 is an important subfamily of the UGTs family and has garnered considerable attention in recent years. Members of the UGT73 subfamily exhibit unique and crucial functions in various plant processes including growth and development, metabolic regulation, and environmental adaptation. Overall, UGT73 proteins are characterized by a modular architecture in which multiple functional regions act in concert to fulfill their biological roles in catalyzing glycosylation reactions. The UGT73 family of proteins possesses a conserved UGT-fold structure, comprising an N-terminal substrate recognition domain and a C-terminal sugar donor-binding domain. The C-terminus of UGT73 proteins is a highly conserved sequence of approximately 44 amino acids, known as the PSPG box [70]. The PSPG box exhibited 60–80% sequence similarity among UGT73 members derived from diverse plant species. Taking members of the UGT73 family in *Arabidopsis thaliana* as an example, the sequence alignment analysis (Figure 3) revealed a high degree of identity at key amino acid positions within the PSPG box regions. This conserved motif plays a crucial role in the functionality of UGT73 proteins, which are primarily responsible for specific binding to UDP-sugar donors [74]. The PSPG box contains at least ten highly conserved amino acid residues that stabilize interactions with UDP-sugar donors, with hydrogen bonding serving as a crucial mechanism. Studies have demonstrated that the conserved aspartic acid (Asp), histidine (His), and arginine (Arg) residues within this motif mediate specific binding to donor molecules, such as UDP-glucose, through the formation of hydrogen and ionic bonds in UGT73 proteins [75].

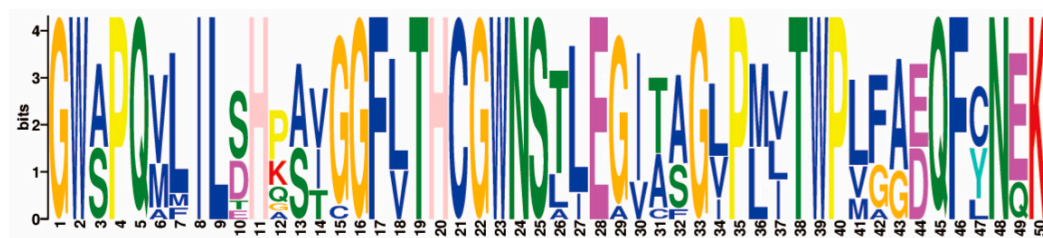


Figure 3. Protein conserved sequence of the AtUGT73 family motif (PSPG box). Based on MAGE7 software, multiple sequence alignment was performed on the UGT73 family genes of *Arabidopsis thaliana*, and the conserved protein sequences of the motif (PSPG box) of the UGT73 family in *Arabidopsis thaliana* were obtained.

Beyond the conserved PSPG box motif, other regions of the UGT73 proteins exhibit a certain level of sequence variability, constituting the variable region of UGT73. The amino acid sequences within this variable region display considerable divergence among different UGT73 members, which confers upon UGT73 subfamily members their specificity for recognizing and binding diverse acceptor substrates [76]. During flavonoid glycosylation, UGT73 members from different plant species recognize and bind flavonoid acceptor molecules with varying structures, a capability that is primarily attributed to the diversity of amino acid sequences within their variable regions. The structural flexibility of the variable region enables UGT73 to accommodate a wide range of acceptor substrate conformations. Consequently, UGT73 participates in the glycosylation of complex and diverse plant secondary metabolites, thereby providing a molecular foundation for the structural and functional diversity of these compounds [77].

5. Substrate Specificity and Catalytic Mechanisms of UGT73 Family Glycosyltransferases

5.1. Complex Substrate Spectrum of UGT73 Family Glycosyltransferases

Members of the UGT73 family of glycosyltransferases possess a broad substrate spectrum, enabling the glycosylation of plant secondary metabolites, phytohormones, and xenobiotics and exhibit remarkable catalytic promiscuity and structural selectivity (Tables 1–3). In terpenoid metabolism, *UGT73DY2* from *Paris polyphylla* specifically catalyzes the 4'-O-rhamnosylation of steroidal diglycosides (e.g., polyphyllin V and VI) to produce the pharmaceutically active compound polyphyllin III. This catalytic activity critically depends on the precise recognition of both the UDP-rhamnose donor and the steroidal backbone [78]. Similarly, *UGT73C1* and *UGT73C5* from *Arabidopsis thaliana* can sequentially glycosylate steviol to produce the high-value sweeteners, rebaudiosides A and M [79]. Furthermore, UGT73 family members (e.g., *UGT73C7*) can modify phenolic acids, including *p*-coumaric acid and ferulic acid, thereby enhancing plant immune responses by modulating phenylpropanoid metabolic flux [80]. In flavonoid metabolism, the UGT73 family demonstrates multi-site glycosylation capabilities. Specifically, in *Arabidopsis*, *UGT73C6*, *UGT73B1*, and *UGT73B2* have all been identified as flavonoid 7-O-glucosyltransferases [81,82], whereas *UGT73A17* catalyzes the 7-O- or 3-O-glucosylation of flavonols (e.g., kaempferol and quercetin), flavones (e.g., apigenin), and flavanones (e.g., naringenin) [83,84]. In isoflavone metabolism, the enzymes *UGT73F2* and *UGT73P2* from soybean (*Glycine max*), along with *UGT73C20* and *UGT88E19* from *Arabidopsis*, efficiently catalyze the 7-O-glucosylation of genistein and daidzein, significantly increasing isoflavone glycoside content [7,85]. Furthermore, *UGT73CD1* specifically modifies irigenin to iridin, highlighting its function as a *7-O*-glycosyltransferase [86]. Additionally, the UGT73 family participates in triterpenoid saponin biosynthesis [86]. Specifically, *UGT73C10–UGT73C13* from *Barbarea vulgaris* catalyze the 3-O-glucosylation of oleanolic acid and hederagenin [87,88], while overexpression of *PgUGAT252645* in ginseng (*Panax ginseng*) significantly increases the accumulation of ginsenoside Ro [89]. Heterologous expression of *UGT73C11* in yeast and tobacco (*Nicotiana benthamiana*) cooperates with oxidosqualene cyclase and cytochrome P450 enzymes to generate 3-O-monoglucosylated sapogenins, indicating its essential role in triterpenoid glycosylation [90]. Additionally, transcription of the licorice (*Glycyrrhiza uralensis*) *UGT73P12* gene is regulated by H3K4me3 epigenetic modification, and its enhanced expression in root tissues through chromatin remodeling promotes glycyrrhizin biosynthesis [24]. Because of their substrate promiscuity, regioselectivity, and structural specificity, the UGT73 family holds promise for applications in plant metabolic engineering and natural product synthesis.

Table 1. The impact on the expression/activity of UGT73s in plants with known flavonols substrate(s).

UGT Isoform	Plant Species	Substrate(s)	Action	Physiological Effects	Ref.
UGT73C6	<i>Arabidopsis thaliana</i>	Flavonol	Overexpression	The involvement of the synthesis of the quercetin-rhamnoside-glucoside	[91]
ScUGT73B4	<i>Solanum tuberosum</i>	flavonoids	Overexpression	cold tolerance	[92]
UGT73B23, UGT73B24	<i>Fragaria × ananassa</i>	3-hydroxycoumarin	In vitro catalytic activities	Contributing to APG glucosides accumulated during the ripening of strawberry fruit	[93]

Table 1. Cont.

UGT Isoform	Plant Species	Substrate(s)	Action	Physiological Effects	Ref.
UGT733C6, UGT73B2	<i>Arabidopsis thaliana</i>	Naringenin	In vitro catalytic activities	Promoted (2S)-naringenin production	[94]
UGT73A17	<i>Camellia sinensis</i>	Quercetin	In vitro catalytic activities	Involved in heat response and quality of tea plant	[95]
CsUGT73AC15	<i>Camellia sinensis</i>	Rutin, Kaempferol 3-O-Rutinoside	Transiently suppress	Enhancing flavor profiles of tea plants	[96]
AhUGT75A (UGT73CG33)	<i>Arachis hypogaea</i>	Naringenin	Overexpression	Higher tolerance to salt and drought stresses	[39]
UGT73AC11	<i>Glycyrrhiza uralensis</i>	Liquiritigenin	In vitro catalytic activities	Broad-spectrum flavonoid biocatalyst	[97]
UGT73A18	<i>Panax ginseng</i>	Kaempferol	In vitro catalytic activities	Involved in the formation of flavonol glycosides in leaves and stems	[98]

Table 2. The impact on the expression/activity of UGT73s in plants with known Terpenoids substrate(s).

UGT Isoform	Plant Species	Substrate(s)	Action	Physiological Effects	Ref.
UGT73C10/11	<i>Barbarea vulgaris</i>	Oleanolic acid, Hederagenin, Betulinic acid	In vitro catalytic activities	Enhance plant insect pest resistance	[26]
AmGT11/72	<i>Astragalus membranaceus</i>	Cycloastragenol	In vitro catalytic activities	Contributing to the 3-O-glycosylation of cycloastragenol, giving rise to astraverrucin I or 5 astramembrannin II	[99]
UGT73C1	<i>Arabidopsis thaliana</i>	Steviol	In vitro catalytic activities	Contributing to the glycosylation of steviol	[83]
UGT73AM3	<i>Cucumis sativus</i>	Cucurbitacin C	In vitro catalytic activities	Contributing to the glycosylation of Cucurbitacin C, giving rise to CuC	[100]
GmUGT73F2	<i>Glycine max</i>	Product of GmSSAT1	In vitro catalytic activities	3-O- β -glucopyranoside Most notably in the pods and pod shells where soyasaponins accumulate	[101]
UGT73C11	<i>Barbarea vulgaris</i>	Glycyrrhetinic acid	In vitro catalytic activities	Improved significantly the water solubility and antibacterial activity of the parent GA	[102]
UGT73AH1	<i>Centella asiatica</i>	Asiatic acid	In vitro catalytic activities	Catalyzes the glycosylation of a ursane-type triterpene produces asiatic acid monohexoside	[103]
UGT73F17, UGT73F24, UGT73C33, UGT73F15	<i>Glycyrrhiza uralensis</i>	Glycyrrhizic acid	In vitro catalytic activities	Efficient biocatalyst to specifically	[104–106]
AeUGT73CB3	<i>Aralia elata</i>	Calenduloside E	In vitro catalytic activities	Efficient biocatalyst to specifically	[107]
UGT73F3	<i>Medicago truncatula</i>	Hederagenin	Knockout	Stunted in growth compared	[108]

Table 3. The impact on the expression/activity of UGT73s in plants with other and unknown substrate(s).

UGT Isoform	Plant Species	Substrate(s)	Action	Physiological Effects	Ref.
UGT73C5	<i>Arabidopsis thaliana</i>	Deoxynivalenol	Overexpression	Deoxynivalenol tolerance	[109]
UGT73B4	<i>Arabidopsis thaliana</i>	Trinitrotoluene	Overexpression	TNT tolerance and enhanced root growth	[110]
UGT73B3/5	<i>Arabidopsis thaliana</i>	Unknown	Knockout	<i>Pseudomonas syringae</i> infection susceptibility and ROS accumulation	[111,112]
UGT73C	<i>Aegilops tauschii</i>	Unknown	Upregulation upon mesosulforun-methyl treatment	Herbicide tolerance	[113]
UGT73C7	<i>Arabidopsis thaliana</i>	p-coumaric acid, ferulic acid	Overexpression	significantly increased resistance to <i>Pseudomonas syringae</i>	[80]
UGT73B1, UGT73B2, UGT73B4, UGT73B5, UGT73C1, UGT73C7, UGT73D1	<i>Arabidopsis thaliana</i>	Unknown	Upregulation upon fenclorim treatment	Herbicide tolerance	[114]
UGT73B,	<i>Alopecurus myosuroides</i>	Unknown	Up/Downregulation upon fenaxaprop-P-ethyl treatment	No effect	[115]
UGT73B2, UGT73B3, UGT73B4	<i>Arabidopsis thaliana</i>	Unknown	Overexpression upon ibuprofen treatment	Ibuprofen tolerance and enhanced metabolism	[116]
UGT73B6	<i>Rhodiola sachalinensis</i>	p-coumaric acid	Overexpression	Contribute to salidoside 3 synthesis	[117]
UGT73CE1	<i>Paris polyphylla</i>	Diosgenin 3-O-glucoside	In vitro catalytic activities	Antifungal activity against	[118]
UGT73A24, UGT73A25	<i>Nicotiana benthamiana</i>	N-feruloyl tyramine	Transiently suppress	Enhance plant disease resistance	[119]

5.2. Multi-Site Catalysis in UGT73 Family Glycosyltransferases

When the UDP–sugar donor binds to the UGT73 protein, conformational adjustments occur not at an isolated binding site, but through synergistic changes within a “composite substrate-binding region”. This region consists of two functionally linked units: the UDP–sugar binding sub-site and the sugar acceptor binding sub-site. These two units undergo “coordinated adaptation” via flexibility of the protein backbone. The UDP–sugar binding sub-site responds first to donor binding, undergoing fine conformational tuning that primes the enzyme for subsequent interactions. The acceptor substrate, which is the target of glycosylation, determines the binding efficiency of UGT73 based on its structural and chemical properties. The acceptor substrate specificity of different UGT73 members is dictated by variable regions of the protein [26]. Sequence variations in these regions not only enable UGT73s to recognize structurally diverse acceptors but also allow conformational plasticity within the acceptor binding sub-site to achieve precise accommodation. After UDP–sugar binding induces conformational changes in the donor sub-site, these changes are allosterically transmitted to the acceptor binding sub-site, prompting it to adjust its conformation via an induced-fit mechanism to form a binding pocket complementary to the acceptor substrate (e.g., flavonoids) [120]. For instance, during flavonoid glycosylation, the acceptor binding sub-site of UGT73 undergoes conformational adjustments to accurately recognize specific structural features of the flavonoid molecule. Simultaneously, the UDP–sugar binding sub-site maintains stable interactions with the donor. This coordination ensures the directed transfer of the glycosyl group to the specific target hydroxyl on the flavonoid, resulting in a flavonoid glycoside with defined structure and function. The structural features of UGT73 are essential for supporting efficient catalysis. Its C-terminal

PSPG box constitutes the core of the UDP–sugar binding sub-site [80]. Several conserved amino acid residues within this motif form hydrogen bonds and electrostatic interactions with the UDP–sugar donor. The conformational stability of the PSPG box directly affects the function of the donor sub-site—mutations of key residues within the PSPG box can not only reduce affinity for the UDP–sugar donor but may also disrupt the conformational synergy between the donor and acceptor sub-sites, ultimately leading to reduced or complete loss of catalytic activity [79]. The variable regions of UGT73 largely form the acceptor binding sub-site. Their structural flexibility is crucial for the “coordinated adaptation” between the two sub-sites. In the later stages of the reaction, following glycoside formation, both the donor and acceptor sub-sites undergo synchronized conformational resetting. Through backbone flexibility, the enzyme returns to its initial state, preparing for the next catalytic cycle. Throughout this process, conformational changes in the two sub-sites follow a dynamic sequence: initial binding-triggered change in the UDP–sugar sub-site—precise adaptation of the acceptor sub-site—coordinated reset of both. This functional coupling ensures the ordered binding of glycosyl donor and acceptor, stabilizes the covalent intermediate, and enables precise glycosyl transfer.

The functional diversity of UGTs is governed by their catalytic regioselectivity and substrate-recognition mechanisms. Research has demonstrated that six enzymes of the UGT73C subfamily concurrently glucosylate pentacyclic triterpenoid sapogenins at both the C-3 and C-28 positions [121], whereas UGT73AD1 exhibits strict regioselectivity, exclusively catalyzing the C-28 carboxyl glucosylation of asiatic acid and hydroxyasiatic acid to participate in centelloside biosynthesis [122]. Furthermore, distinct UGTs exhibit pronounced positional preferences for benzoate glucosylation; UGT78D2, UGT71B1, UGT73B3, and UGT89B1 exclusively modify the 4-OH position, whereas UGT74F1 and UGT74F2 selectively target the 2-OH position [123]. During glycan chain elongation, UGT73F4 and UGT73F2 are responsible for transferring xylose and glucose, respectively, to the C-22 arabinosyl residue [87,88], whereas GmSGT2 (a UGT73 family member) displays rigorous specificity toward pentacyclic triterpenoid backbones, with its substrate recognition mechanism elucidated through molecular docking [124]. Notably, UGTs exhibit residue-dependent specificity for sugar donor selection. For instance, licorice GuUGT73P12 specifically recognizes UDP–glucuronic acid (UDP–GlcA) via electrostatic interactions between Arg32 and its carboxyl group. Mutation of this residue markedly diminishes its catalytic efficiency toward UDP–glucose (UDP–Glc) and UDP–galactose (UDP–Gal), while altering substrate specificity [125]. Collectively, these findings elucidate how UGTs regulate the structural modifications and bioactivities of specialized metabolites through precise residue recognition and sugar donor-binding mechanisms, thereby providing a molecular foundation for the rational design of glycosyltransferases.

5.3. Distinct Catalytic Mechanisms of UGT73 Family Glycosyltransferases

The glycosyltransferase reaction catalyzed by the UGT73 family follows the classic double-displacement (ping-pong) mechanism [26]. Its core feature involves the formation of a glycosyl-enzyme covalent intermediate via two successive nucleophilic attacks, accompanied by two inversions of anomeric carbon configuration, ultimately resulting in net retention of the glycosyl stereochemistry. The entire process can be divided into three tightly coupled and highly ordered stages, each mediated by specific structural domains (such as the C-terminal PSPG motif) and conserved amino acid residues to ensure high efficiency and precision [118]. Stage 1: Glycosyl Donor Binding and Covalent Intermediate Formation. UDP–sugar (e.g., UDP–glucose, UDP–glucuronic acid) acts as an activated glycosyl donor and is initially recognized and bound specifically by the C-terminal PSPG motif. Through its highly conserved amino acid sequence, the PSPG motif utilizes residues such

as Asp, His, and Arg to form hydrogen bonds, ionic interactions, and other non-covalent bonds with the phosphate group and sugar moiety of the UDP-sugar, anchoring it stably within the active site to form an enzyme-donor complex. The high-energy phosphodiester bond between the sugar and UDP provides the driving force for the subsequent transfer. A conserved nucleophilic residue in the active site (often aspartate Asp or glutamate Glu) then attacks the anomeric carbon (C1) of the sugar donor via its carboxylate group ($-\text{COO}^-$), leading to cleavage of the glycosyl-UDP bond and release of UDP. Simultaneously, a covalent bond forms between the anomeric carbon and the nucleophilic residue, generating a glycosyl-enzyme covalent intermediate (e.g., a glycosyl-Asp intermediate). This step is accompanied by the first inversion of the anomeric configuration (α - or β -). Stage 2: Intermediate Stabilization and Acceptor Binding, After the glycosyl-enzyme covalent intermediate is formed, the UGT73 active site stabilizes its conformation through non-covalent interactions such as hydrogen bonds and electrostatic forces, preventing premature dissociation of the glycosyl group. The sugar acceptor (e.g., flavonoids, triterpenoid sapogenins) then docks precisely into the active site, positioning its nucleophilic group (e.g., hydroxyl $-\text{OH}$, carboxyl $-\text{COOH}$) toward the anomeric carbon of the glycosyl intermediate. The micro-environment of the active site (including local charge distribution and hydrophobicity) further optimizes spatial compatibility, preparing for the subsequent glycosyl transfer [126]. Stage 3: Glycosyl Transfer and Enzyme Regeneration, Once the sugar acceptor is properly positioned, specific residues in the active site (e.g., Asp187, His210) act synergistically as acid-base catalysts. Asp187 initially functions as a general base to deprotonate the nucleophilic group of the acceptor (e.g., a hydroxyl), enhancing its nucleophilicity. This activated nucleophile then attacks the anomeric carbon of the glycosyl-enzyme intermediate in a second nucleophilic substitution. His210 serves as a general acid to stabilize the transition state, facilitating cleavage of the covalent bond between the glycosyl group and the enzymatic nucleophile. Concurrently, a new glycosidic bond is formed between the glycosyl group and the acceptor, yielding a well-defined glycosylated product [126]. Finally, the product dissociates from the active site, restoring the enzyme's active conformation. The nucleophilic residue and PSPG motif become accessible again, ready to bind a new UDP-sugar donor and initiate another catalytic cycle [127].

Isotope labeling studies provided an in-depth catalytic kinetic analysis of *Camellia sinensis* CsUGT73AC15. During rutin glycosylation, this enzyme exhibited a glucosyl transfer rate constant (k_{cat}) of 12.3 s^{-1} and a Michaelis constant (K_{m}) of 0.15 mM. An elevated k_{cat} value indicates rapid substrate turnover, whereas a low K_{m} value reflects strong binding affinity toward rutin. Collectively, these kinetic parameters demonstrate that CsUGT73AC15 efficiently catalyzes rutin glycosylation at low substrate concentrations [96]. The catalytic mechanisms of the UGT73 family of glycosyltransferases are modulated by multiple factors. Dynamic conformational changes play essential roles during catalysis, and molecular dynamic simulations have revealed significant structural rearrangements in the active site throughout the catalytic cycle to accommodate substrate binding, glycosyl transfer, and product release [128]. Concurrently, interactions with other proteins (e.g., chaperones) may regulate catalytic activity by maintaining proper enzyme conformation or modulating the active-site microenvironment, thereby influencing catalytic efficiency and substrate specificity.

6. Diverse Biological Functions of UGT73 Family Glycosyltransferases in Plants

6.1. Influence of UGT73 Family Glycosyltransferases on Plant Growth and Development

The UGT73 family of glycosyltransferases broadly regulates plant growth and development through glycosylation, modulating processes, such as fruit ripening, floral

pigmentation, secondary metabolism, and environmental adaptation (Figure 4). During fruit development, transcript levels of *UGT71K3* and *UGT73B24* were significantly upregulated at the ripening stage, exhibiting 83-fold and 113-fold higher expression in red versus green fruits, respectively, indicating their critical roles in fruit maturation and pigment accumulation in strawberries (*Fragaria × ananassa*) [93]. UGT73 members can also glycosylate volatile compounds and modulate flavor and aroma to enhance product quality and commercial value in strawberries and *Aralia elata* [129]. During floral organ development, members of the UGT73 family participate in anthocyanin glycosylation, which influences floral coloration and stability. For instance, *Petunia hybrida* UGT73 glycosyltransferases catalyze the formation of stable anthocyanin glycosides, which intensify flower pigmentation to attract pollinators, while protecting anthocyanins from oxidative damage to maintain physiological functions [54]. Furthermore, the UGT73 family of glycosyltransferases critically regulates secondary metabolism and stress responses in plants. For instance, *Camellia sinensis* UGT73A17 synthesizes diverse flavonoid glucosides to mediate heat adaptation and enhance tea quality [95], whereas *Medicago truncatula* UGT73F3 catalyzes C-28 glycosylation of triterpenoid saponins (e.g., hederagenin), with loss-of-function mutations disrupting triterpenoid homeostasis and suppressing plant growth [87]. These studies have elucidated how UGT73 family glycosyltransferases regulate phytohormones, specialized metabolites, and environmental adaptation via glycosylation, thereby providing key targets for rational crop improvement and stress-resilient breeding.

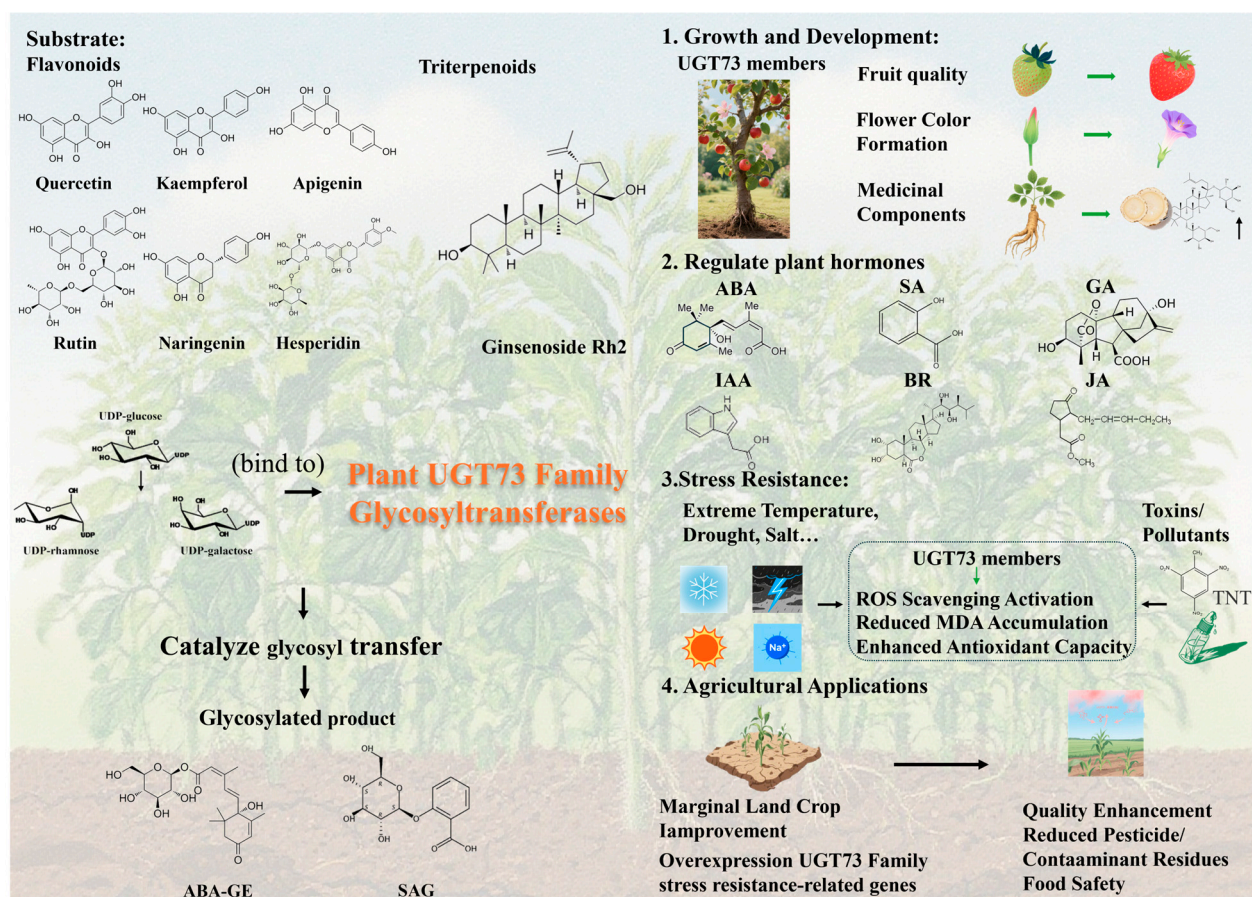


Figure 4. Catalytic Mechanism of Plant UGT73 Family Glycosyltransferases and Their Roles in Plant Physiology and Agricultural Applications. The image is structured into left and right panels. The left panel illustrates the catalytic process of the UGT73 family, while the right panel demonstrates the roles of the UGT73 family in plant growth and development, hormone regulation, and stress resistance, along with their application prospects.

6.2. Regulatory Roles of UGT73 Family Glycosyltransferases in Phytohormone Homeostasis

The UGT73 family of glycosyltransferases serves as a core regulator of phytohormone homeostasis by modulating hormone activity and signaling through glycosylation (Figure 4). Research has demonstrated that Arabidopsis UGT73C subfamily members exhibit broad substrate specificity; *UGT73C1*, *UGT73C5* and *UGT85A1* catalyze the O-glucosylation of cytokinins (e.g., trans-zeatin), whereas *UGT73C11* specifically glycosylates gibberellic acid (GA) to form GA-3-O-glucoside [81,82,124]. Notably, *UGT73C5* and *UGT73C6* regulate brassinosteroid (BR) metabolism through two mechanisms: catalyzing 23-O-glycosylation for direct BR inactivation, while forming BR-malonyl glycosides to prevent degradation, and their overexpression induces characteristic BR-deficient phenotypes [7]. In defense hormone regulation, *UGT73B3/73B5* enhances the expression of the pathogenesis-related gene PR1 via salicylic acid-dependent pathways, with mutants exhibiting significantly reduced resistance to *Pseudomonas syringae*. Conversely, *UGT73C4* activates disease resistance signaling by promoting salicylic acid and jasmonic acid accumulation. Exogenous methyl jasmonate induces the upregulation of *UGT73K1* and related genes, thereby catalyzing the glycosylation of defense compounds, such as flavonoids [7]. Additionally, UGT73s fine-tune seed germination via abscisic acid (ABA) glycosylation to release dormancy constraints [130]. Collectively, these findings reveal how UGT73 glycosyltransferases integrate plant growth and stress responses through spatiotemporally specific hormone-glycosylation networks.

6.3. Regulatory Impact of UGT73 Family Glycosyltransferases on Plant Stress Resistance

The UGT73 family of glycosyltransferases plays a key role in plant stress resistance by modulating metabolite activity and cellular homeostasis through glycosylation (Figure 4). In abiotic stress responses, Arabidopsis *UGT73B3/B5* and *UGT74E2* show inducible expression under osmotic, oxidative, and salt stress [88]. Rice (*Oryza sativa*) *UGT73C3* enhances heat tolerance by scavenging ROS [131], while tomato (*Solanum lycopersicum*) overexpressing *SlUGT73C1* significantly enhance salt and drought tolerance through elevated superoxide dismutase/peroxidase activities, reduced malondialdehyde content, and upregulation of stress-responsive genes [114,132]. Similarly, *Solanum commersonii* *ScUGT73B4* enhances freezing tolerance through cold-induced flavonoid glycosylation to boost antioxidant capacity [92], whereas peanut (*Arachis hypogaea*) *AhUGT75A* and soybean *GmUGT73F2/F4* improve drought and salt resistance by reducing malondialdehyde accumulation and activating ROS scavenging systems [133,134]. In Arabidopsis, *UGT74B4* and *UGT73C1* overexpression enhances TNT detoxification and promotes root growth [110]. Studies have demonstrated that *Nicotiana benthamiana* *NbUGT73A24/25* can catalyze the biosynthesis of phytoalexins and flavonol glycosides to fortify the cell walls against pathogens [119]. Additionally, Arabidopsis *ugt73b3/73b5* mutants exhibited reduced resistance to *Pseudomonas syringae* and heightened ROS accumulation upon pathogen challenge, indicating glycosylation-mediated control of ROS scavenging [84,114,135]. In mycotoxin detoxification, Arabidopsis *AtUGT73C5* and barley (*Hordeum vulgare*) *HvUGT13248* reduce deoxynivalenol (DON) toxicity via glycosylation [7]. Collectively, the UGT73 family of glycosyltransferases establish a multilayered stress resistance network by glycosylating metabolites (e.g., flavonoids, phytoalexins, and toxins), regulating ROS homeostasis, and modulating stress-responsive gene expression, which play pivotal roles in plant adaptation to biotic and abiotic stresses.

7. Application Prospects of Plant UGT73 Family Glycosyltransferases

The UGT73 family of glycosyltransferases exhibits significant potential in plant metabolic and enzyme engineering, with their functional properties offering innovative

avenues for synthetic biology and green chemistry. The structural plasticity of UGT73 enzymes provides a foundation for the rational design of novel biocatalysts. By leveraging their conserved PSPG domain and malleable substrate-binding pockets, their substrate scope and catalytic efficiency can be expanded through site-directed mutagenesis (e.g., Tyr202Glu mutation in UGT73C1) or domain fusion (e.g., coupling with cytochrome P450 monooxygenases) [78,136]. For example, fusing the rhamnosyltransferase activity of UGT73DY2 with glycoside hydrolases enables the engineering of artificial enzyme systems for sequential multistep glycosylation reactions [78]. In plant metabolic engineering, the directed regulation of the UGT73 family of glycosyltransferases significantly enhances the synthesis efficiency of pharmaceutically active compounds. For instance, targeted UGT73 regulation has been widely applied in medicinal compound biosynthesis: heterologous expression of UGT73DY2 in *Paris polyphylla* drives high-yield accumulation of anticancer steroidal saponin precursors [78]; in *Rhodiola crenulata*, UGT73B6, UGT72B14 and UGT74R1 collectively synthesize salidroside; while Arabidopsis-derived AtUGT73C5, AtUGT73C6 and AtUGT85A1 (the latter exhibiting highest catalytic efficiency and regioselectivity) catalyze tyrosol glucosylation to form salidroside [137]. Furthermore, UGT73CD1 functions as a 7-O-glycosyltransferase that specifically converts irigenin to iridin, whereas overexpression of PgUGAT252645 in ginseng substantially increases ginsenoside Ro production [89]. Notably, UGT73AD1 demonstrates strict substrate specificity, exclusively catalyzing the C28-carboxyl glucosylation of asiatic acid and its derivatives, and has been identified as a triterpenoid carboxylic acid 28-O-glycosyltransferase [122]. These findings reveal the versatile catalytic functions of UGT73 in saponin/flavonoid glycoside biosynthesis and provide pivotal molecular targets for the metabolic engineering of medicinal plants.

The UGT73 family of glycosyltransferases plays multifaceted roles in phytoremediation by enhancing plant detoxification capacity through glycosyl-conjugation of toxic compounds. Studies have demonstrated that Arabidopsis UGT73C1, UGT73C6, UGT73B2 and UGT73B5 respond to TNT contamination by specifically upregulating their expression to convert TNT derivatives (2- and 4-hydroxylaminodinitrotoluenes) into low-toxicity conjugates, providing a molecular basis for the bioremediation of explosive-contaminated soils [110]. Furthermore, UGT73 family glycosyltransferases exhibit exceptional substrate promiscuity. For example, UGT73C7 coupled with fluorescent reporter systems enables real-time biosensing of herbicide residues and heavy metal stress in plants [110]. Notably, in weed resistance mechanisms, induced expression of UGT73C1 in penoxsulam-resistant *Cyperus difformis* population GX-35 suggests its role in metabolic detoxification conferring resistance to acetolactate synthase-inhibiting herbicides [138]. These findings expand the environmental applications of UGT73 and identify novel targets for managing resistant weeds.

8. Conclusions and Perspectives

As pivotal members of the plant UGT Family D, UGT73 family glycosyltransferases have emerged as a major research focus in plant molecular biology and agricultural applications because of their diverse roles in plant growth and development, hormonal homeostasis regulation, and stress responses. Research progress in this field has considerable implications for deciphering plant adaptive mechanisms and advancing crop genetic improvements. At the biological functional level, UGT73 family glycosyltransferases affect plant life activities through multiple pathways: (1) In growth and development, the accumulation of flavonoid glycosides catalyzed by UGT73 family glycosyltransferases enhances fruit quality [129], regulates flower color stability [54], and participates in the biosynthesis of bioactive compounds such as ginsenosides in medicinal plants like ginseng (*Panax ginseng*) [25,89] which had high economic value. (2) In terms of hormone regulation,

UGT73 family glycosyltransferases dynamically balance hormone activity and regulate growth, development, and stress responses by glycosylating hormones, such as IAA, GA, and ABA [64,65,130]. (3) In terms of stress resistance and defense, when facing stresses, such as drought and pathogen infection, the UGT73 family of glycosyltransferases can accelerate the synthesis of antioxidant substances to scavenge reactive oxygen species or achieve detoxification by glycosylating exogenous toxins. They also regulate stress hormone signal transduction and enhance stress resistance [84,92,110,114,119,131–135]. (4) In agricultural production, the UGT73 family of glycosyltransferases has significant application prospects. Cloning stress resistance-related UGT73 family glycosyltransferase genes and expressing them in crops through transgenesis or gene editing technologies can enhance crop adaptability to marginal lands such as saline-alkali and arid areas [114]. Precise regulation of the expression of its members can optimize the synthesis of metabolites, such as flavonoids and steroids, thereby improving the nutritional and medicinal value of agricultural products [89]. Additionally, their potential role in reducing pesticide residues and pollutants supports green agriculture and food safety [110].

Recent studies have partially elucidated the functions of the UGT73 family of glycosyltransferases; however, their broader biological significance remains underexplored. In vivo functional research is necessary to conduct full-spectrum metabolite analysis on plants overexpressing UGT73 family glycosyltransferase genes, track the dynamic changes in metabolites, and thereby analyze their impacts on plant growth and development (such as plant height and flowering phenology), as well as environmental stress responses (such as drought tolerance and pathogen resistance) [80,86]. This is key to connecting molecular functions to physiological phenotypes. Currently, the UGT73 family of glycosyltransferases faces several unresolved core scientific questions. The substrate specificity of their catalytic activity remains unclear, with limited evidence of their preference for particular metabolites and an insufficient understanding of species-specific divergence in substrate selection among different members [139]. In addition, critical gaps exist in the elucidation of the molecular mechanisms underlying their physiological functions. It is unknown whether the highly expressed members participate in key biological processes or their associated upstream and downstream pathways [112]. Furthermore, the collaborative dynamics within the family, such as the functional relationships among multiple members and their coordinated responses to environmental signals, remain poorly characterized. Systematic investigations are required to address these knowledge gaps and advance our understanding of UGT73-mediated glycosylation in plant metabolism and stress adaptation.

To address these challenges, a multidimensional strategy integrating traditional molecular biology, advanced omics technologies, and artificial intelligence (AI) is recommended [5,140,141]. For basic functional validation, CRISPR/Cas9-generated knockout lines should be combined with metabolomic and transcriptomic analyses to clarify gene expression patterns, subcellular localization, and metabolic associations. Promoter bioinformatic analyses can further identify regulatory elements to support precise expression modulation [7]. To enhance research efficiency, AI-based approaches can be employed at multiple stages. During substrate recognition, deep learning models trained on existing data can accelerate the prediction of substrate specificity, which can then be experimentally validated. For functional interpretation, computational algorithms can help identify key metabolic pathways, while image recognition tools enable high-throughput quantification of phenotypic variations, thus strengthening the association between metabolic changes and organismal phenotypes. In synthetic biology applications, creating mutant libraries and training predictive models with high-throughput data will facilitate the identification of critical residues guiding enzyme engineering [142]. These efforts will not only systematically reveal the functional roles and biological significance of UGT73 glycosyltransferases

but also provide a “gene-to-phenotype” research framework applicable to the broader plant UGT superfamily. Furthermore, this integrated approach will support the redesign of plant metabolic pathways through synthetic biology and contribute to the development of improved crop varieties.

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References

1. Tang, H.; Wang, Q.; Xie, H.; Li, W. The function of secondary metabolites in resisting stresses in horticultural plants. *Fruit Res.* **2024**, *4*, e021. [\[CrossRef\]](#)
2. Rahimi, S.; Kim, J.; Mijakovic, I.; Jung, K.H.; Choi, G.; Kim, S.C.; Kim, Y.J. Triterpenoid-biosynthetic UDP-glycosyltransferases from plants. *Biotechnol. Adv.* **2019**, *37*, 107394. [\[CrossRef\]](#) [\[PubMed\]](#)
3. Wu, B.; Liu, X.; Xu, K.; Zhang, B. Genome-wide characterization, evolution and expression profiling of UDP-glycosyltransferase family in pomelo (*Citrus grandis*) fruit. *BMC Plant Biol.* **2020**, *20*, 459. [\[CrossRef\]](#)
4. Cantarel, B.L.; Coutinho, P.M.; Rancurel, C.; Bernard, T.; Lombard, V.; Henrissat, B. The Carbohydrate-Active EnZymes database (CAZy): An expert resource for Glycogenomics. *Nucleic Acids Res.* **2009**, *37*, D233–D238. [\[CrossRef\]](#)
5. Wu, J.; Zhu, W.; Shan, X.; Liu, J.; Zhao, L.; Zhao, Q. Glycoside-specific metabolomics combined with precursor isotopic labeling for characterizing plant glycosyltransferases. *Mol. Plant* **2022**, *15*, 1517–1532. [\[CrossRef\]](#)
6. Sirirungruang, S.; Blay, V.; Rodriguez, E.P.; Scott, Y.F.; Vu, K.M.; Barnum, C.R.; Opgenorth, P.H.; Kong, F.; Li, Y.; Fiehn, O.; et al. A substrate-multiplexed platform for profiling enzymatic potential of plant family 1 glycosyltransferases. *Nat. Commun.* **2025**, *16*, 6366. [\[CrossRef\]](#)
7. Yu, A.D.; Liu, L.; Long, R.C.; Kang, J.M.; Chen, L.; Yang, Q.C.; Li, M.N. Functions and application prospects of plant UDP-glycosyltransferases (UGT). *Plant Physiol. J.* **2022**, *58*, 631–642. (In Chinese) [\[CrossRef\]](#)
8. Yang, F.; Zhang, L.; Zhang, X.; Guan, J.; Wang, B.; Wu, X.; Song, M.; Wei, A.; Liu, Z.; Huo, D. Genome-wide investigation of UDP-Glycosyltransferase family in Tartary buckwheat (*Fagopyrum tataricum*). *BMC Plant Biol.* **2024**, *24*, 249. [\[CrossRef\]](#)
9. Wang, J.; Hu, Y.; Guo, D.; Gao, T.; Liu, T.; Jin, J.; Zhao, M.; Yu, K.; Tong, W.; Ge, H.; et al. Evolution and functional divergence of glycosyltransferase genes shaped the quality and cold tolerance of tea plants. *Plant Cell* **2024**, *37*, koae268. [\[CrossRef\]](#) [\[PubMed\]](#)
10. Knoch, E.; Sugawara, S.; Mori, T.; Nakabayashi, R.; Saito, K.; Yonekura-Sakakibara, K. UGT79B31 is responsible for the final modification step of pollen-specific flavonoid biosynthesis in *Petunia hybrida*. *Planta* **2018**, *247*, 779–790. [\[CrossRef\]](#) [\[PubMed\]](#)
11. Zheng, R.; Zhu, Z.; Wang, Y.; Hu, S.; Xi, W.; Xiao, W.; Qu, X.; Zhong, L.; Fu, Q.; Wang, C. UGT85A84 Catalyzes the Glycosylation of Aromatic Monoterpenes in *Osmanthus fragrans* Lour. *Flowers. Front. Plant Sci.* **2019**, *10*, 1376. [\[CrossRef\]](#)
12. Jing, T.; Du, W.; Qian, X.; Wang, K.; Luo, L.; Zhang, X.; Deng, Y.; Li, B.; Gao, T.; Zhang, M.; et al. UGT89AC1-mediated quercetin glucosylation is induced upon herbivore damage and enhances *Camellia sinensis* resistance to insect feeding. *Plant Cell Environ.* **2024**, *47*, 682–697. [\[CrossRef\]](#)
13. Gachon, C.M.; Langlois-Meurinne, M.; Saindrenan, P. Plant secondary metabolism glycosyltransferases: The emerging functional analysis. *Trends Plant Sci.* **2005**, *10*, 542–549. [\[CrossRef\]](#)
14. Zhang, G.Z.; Lin, J.S.; Li, Y.J.; Hou, B.K. Research progress on glycosylation modification of plant hormones. *Acta Bot. Sin.* **2014**, *49*, 515–523. (In Chinese)
15. Jiang, D.; Lin, S.; Xie, L.; Chen, M.; Shi, Y.; Chen, K.; Li, X.; Wu, B.; Zhang, B. UDP-glycosyltransferase PpUGT74F2 is involved in fruit immunity via modulating salicylic acid metabolism. *Hortic. Res.* **2025**, *12*, uhaf049. [\[CrossRef\]](#)
16. Ao, B.; Han, Y.; Wang, S.; Wu, F.; Zhang, J. Genome-Wide Analysis and Profile of UDP-Glycosyltransferases Family in Alfalfa (*Medicago sativa* L.) under Drought Stress. *Int. J. Mol. Sci.* **2022**, *23*, 7243. [\[CrossRef\]](#)

17. Li, H.; Wang, J.; Li, M.; Wu, L.; Rao, W.; Peng, X.; Jiang, H. The ZmHSF08-ZmUGT92A1 module regulates heat tolerance by altering reactive oxygen species levels in maize. *Crop J.* **2024**, *12*, 1437–1446. [\[CrossRef\]](#)
18. Hu, Y.; Zhang, M.; Lu, M.; Wu, Y.; Jing, T.; Zhao, M.; Zhao, Y.; Feng, Y.; Wang, J.; Gao, T.; et al. Salicylic acid carboxyl glucosyltransferase UGT87E7 regulates disease resistance in *Camellia sinensis*. *Plant Physiol.* **2022**, *188*, 1507–1520. [\[CrossRef\]](#) [\[PubMed\]](#)
19. Chen, Y.; Dan, Z.; Li, S. GROWTH REGULATING FACTOR 7-mediated arbutin metabolism enhances rice salt tolerance. *Plant Cell* **2024**, *36*, 2834–2850. [\[CrossRef\]](#)
20. Poppenberger, B.; Fujioka, S.; Soeno, K.; George, G.L.; Vaistij, F.E.; Hiranuma, S.; Seto, H.; Takatsuto, S.; Adam, G.; Yoshida, S.; et al. The UGT73C5 of *Arabidopsis thaliana* glucosylates brassinosteroids. *Proc. Natl. Acad. Sci. USA* **2005**, *102*, 15253–15258. [\[CrossRef\]](#) [\[PubMed\]](#)
21. Husar, S.; Berthiller, F.; Fujioka, S.; Rozhon, W.; Khan, M.; Kalaivanan, F.; Elias, L.; Higgins, G.S.; Li, Y.; Schuhmacher, R.; et al. Overexpression of the UGT73C6 alters brassinosteroid glucoside formation in *Arabidopsis thaliana*. *BMC Plant Biol.* **2011**, *11*, 51. [\[CrossRef\]](#) [\[PubMed\]](#)
22. Yang, Q.; Zhang, Y.; Qu, X.; Wu, F.; Li, X.; Ren, M.; Tong, Y.; Wu, X.; Yang, A.; Chen, Y.; et al. Genome-wide analysis of UDP-glycosyltransferases family and identification of UGT genes involved in abiotic stress and flavonol biosynthesis in *Nicotiana tabacum*. *BMC Plant Biol.* **2023**, *23*, 204. [\[CrossRef\]](#)
23. Liu, Y.P.; Wei, S. Research on the Tea Plant Glycosyltransferase Gene CsUGT73D1. *J. Hainan Norm. Univ.* **2019**, *32*, 268–280. (In Chinese)
24. Nomura, Y.; Seki, H.; Suzuki, T.; Ohyama, K.; Mizutani, M.; Kaku, T.; Tamura, K.; Ono, E.; Horikawa, M.; Sudo, H.; et al. Functional specialization of UDP-glycosyltransferase 73P12 in licorice to produce a sweet triterpenoid saponin, glycyrrhizin. *Plant J.* **2019**, *99*, 1127–1143. [\[CrossRef\]](#)
25. Kang, K.B.; Jayakodi, M.; Lee, Y.S.; Nguyen, V.B.; Park, H.S.; Koo, H.J.; Choi, I.Y.; Kim, D.H.; Chung, Y.J.; Ryu, B.; et al. Identification of candidate UDP-glycosyltransferases involved in protopanaxadiol-type ginsenoside biosynthesis in *Panax ginseng*. *Sci. Rep.* **2018**, *8*, 11744. [\[CrossRef\]](#)
26. Augustin, J.M.; Drok, S.; Shinoda, T.; Sanmiya, K.; Nielsen, J.K.; Khakimov, B.; Olsen, C.E.; Hansen, E.H.; Kuzina, V.; Ekstrom, C.T.; et al. UDP-glycosyltransferases from the UGT73C subfamily in *Barbarea vulgaris* catalyze saponin 3-O-glucosylation in saponin-mediated insect resistance. *Plant Physiol.* **2012**, *160*, 1881–1895. [\[CrossRef\]](#)
27. Zhang, Y.; Zhao, A.; Mu, L.; Teng, X.; Ma, Y.; Li, R.; Lei, K.; Ji, L.; Wang, X.; Li, P. First Clarification of the Involvement of Glycosyltransferase MdUGT73CG22 in the Detoxification Metabolism of Nicosulfuron in Apple. *Plants* **2024**, *13*, 1171. [\[CrossRef\]](#)
28. Bock, K.W. The UDP-glycosyltransferase (UGT) superfamily expressed in humans, insects and plants: Animal-plant arms-race and co-evolution. *Biochem. Pharmacol.* **2016**, *99*, 11–17. [\[CrossRef\]](#)
29. Mackenzie, P.I.; Owens, I.S.; Burchell, B.; Bock, K.W.; Bairoch, A.; Belanger, A.; Fournel-Gigleux, S.; Green, M.; Hum, D.W.; Iyanagi, T.; et al. The UDP glycosyltransferase gene superfamily: Recommended nomenclature update based on evolutionary divergence. *Pharmacogenetics* **1997**, *7*, 255–269. [\[CrossRef\]](#)
30. Wu, C.; Dai, J.; Chen, Z.; Tie, W.; Yan, Y.; Yang, H.; Zeng, J.; Hu, W. Comprehensive analysis and expression profiles of cassava UDP-glycosyltransferases (UGT) family reveal their involvement in development and stress responses in cassava. *Genomics* **2021**, *113*, 3415–3429. [\[CrossRef\]](#)
31. Yang, Y.; Wang, J.; Han, F.; Zhang, J.; Gao, M.; Zhao, Y.; Chen, Y.; Wang, Y. Characterization of UGT71, a major glycosyltransferase family for triterpenoids, flavonoids and phytohormones-biosynthetic in plants. *For. Res.* **2024**, *4*, e035. [\[CrossRef\]](#)
32. Song, Z.; Niu, L.; Yang, Q.; Dong, B.; Wang, L.; Dong, M.; Fan, X.; Jian, Y.; Meng, D.; Fu, Y. Genome-wide identification and characterization of UGT family in pigeonpea (*Cajanus cajan*) and expression analysis in abiotic stress. *Trees-Struct. Funct.* **2019**, *33*, 987–1002. [\[CrossRef\]](#)
33. Wang, F.; Su, Y.; Chen, N.; Shen, S. Genome-Wide Analysis of the UGT Gene Family and Identification of Flavonoids in *Broussonetia papyrifera*. *Molecules* **2021**, *26*, 3449. [\[CrossRef\]](#)
34. Cheng, Y.; Liu, H.; Tong, X.; Liu, Z.; Zhang, X.; Li, D.; Jiang, X.; Yu, X. Identification and analysis of CYP450 and UGT supergene family members from the transcriptome of *Aralia elata* (Miq.) seem reveal candidate genes for triterpenoid saponin biosynthesis. *BMC Plant Biol.* **2020**, *20*, 214. [\[CrossRef\]](#) [\[PubMed\]](#)
35. Feng, Z.; Admas, T.; Cheng, B.; Meng, Y.; Pan, R.; Zhang, W. UGT gene family identification and functional analysis of HvUGT1 under drought stress in wild barley. *Physiol. Mol. Biol. Plants* **2024**, *30*, 1225–1238. [\[CrossRef\]](#)
36. Guan, H.; Zhang, Y.; Li, J.; Zhu, Z.; Chang, J.; Bakari, A.; Chen, S.; Zheng, K.; Cao, S. Analysis of the UDP-Glucosyltransferase (UGT) Gene Family and Its Functional Involvement in Drought and Salt Stress Tolerance in *Phoebe bournei*. *Plants* **2024**, *13*, 722. [\[CrossRef\]](#)
37. Zhao, X.; Feng, Y.; Ke, D.; Teng, Y.; Chen, Y.; Langjia, R. Molecular Identification and Characterization of UDP-glycosyltransferase (UGT) Multigene Family in Pomegranate. *Horticulturae* **2023**, *9*, 540. [\[CrossRef\]](#)

38. Ma, Y.; Song, J.; Sheng, S.; Wang, D.; Wang, T.; Wang, N.; Chen, A.; Wang, L.; Peng, Y.; Ma, Y.; et al. Genome-wide characterization of *Solanum tuberosum* UGT gene family and functional analysis of StUGT178 in salt tolerance. *BMC Genom.* **2024**, *25*, 1206. [\[CrossRef\]](#)
39. Ouyang, L.; Liu, Y.; Yao, R.; He, D.; Yan, L.; Chen, Y.; Huai, D.; Wang, Z.; Yu, B.; Kang, Y.; et al. Genome-wide analysis of UDP-glycosyltransferase gene family and identification of a flavonoid 7-O-UGT (AhUGT75A) enhancing abiotic stress in peanut (*Arachis hypogaea* L.). *BMC Plant Biol.* **2023**, *23*, 626. [\[CrossRef\]](#) [\[PubMed\]](#)
40. Chen, J.; Qiu, X.; Sun, Z.; Luan, M.; Chen, J. Genome-wide analysis of UDP-glycosyltransferase family in *Citrus sinensis* and characterization of a UGT gene encoding flavonoid 1-2 rhamnosyltransferase. *Int. J. Biol. Macromol.* **2024**, *280*, 135752. [\[CrossRef\]](#) [\[PubMed\]](#)
41. Chen, Y.; Fu, M.; Li, H.; Wang, L.; Liu, R.; Liu, Z. Genome-wide characterization of the UDP-glycosyltransferase gene family reveals their potential roles in leaf senescence in cotton. *Int. J. Biol. Macromol.* **2022**, *222*, 2648–2660. [\[CrossRef\]](#)
42. Li, Y.; Li, P.; Wang, Y.; Dong, R.; Yu, H.; Hou, B. Genome-wide identification and phylogenetic analysis of Family-1 UDP glycosyltransferases in maize (*Zea mays*). *Planta* **2014**, *239*, 1265–1279. [\[CrossRef\]](#)
43. Xiao, X.; Lu, Q.; Liu, R.; Gong, J.; Gong, W.; Liu, A.; Ge, Q.; Li, J.; Shang, H.; Li, P.; et al. Genome-wide characterization of the UDP-glycosyltransferase gene family in upland cotton. *3 Biotech* **2019**, *9*, 453. [\[CrossRef\]](#)
44. Shi, D.; Yang, J.; Li, G.; Zhou, Y.; Yao, P.; Shi, Y.; Tian, J.; Zhang, X.; Liu, Q. Genome-Wide Identification of UGT Genes and Analysis of Their Expression Profiles During Fruit Development in Walnut (*Juglans regia* L.). *Horticulturae* **2024**, *10*, 1130. [\[CrossRef\]](#)
45. Ren, C.; Cao, Y.; Xing, M.; Guo, Y.; Li, J.; Xue, L.; Sun, C.; Xu, C.; Chen, K.; Li, X. Genome-wide analysis of UDP-glycosyltransferase gene family and identification of members involved in flavonoid glucosylation in *Chinese bayberry* (*Morella rubra*). *Front. Plant Sci.* **2022**, *13*, 998985. [\[CrossRef\]](#) [\[PubMed\]](#)
46. Kamal, K.A.; Shah, F.A.; Zhao, Y.; Chen, Z.; Fu, S.; Zhu, Z.; Ren, J.; Liu, H. Genome-wide identification of the UGT genes family in *Acer rubrum* and role of ArUGT52 in anthocyanin biosynthesis under cold stress. *BMC Plant Biol.* **2025**, *25*, 288. [\[CrossRef\]](#)
47. Zhou, L.; Chen, X.; Su, W.; Ou, Z.; Qu, Y. Identification of the UGT Family and Functional Validation of MwUGT2 in *Meconopsis wilsonii*. *Plants* **2025**, *14*, 944. [\[CrossRef\]](#)
48. Li, H.; Yang, X.; Lu, M.; Chen, J.; Shi, T. Gene expression and evolution of Family-1 UDP-glycosyltransferases—Insights from an aquatic flowering plant (*Sacred lotus*). *Aquat. Bot.* **2020**, *166*, 103270. [\[CrossRef\]](#)
49. Li, Y.; Li, P.; Zhang, L.; Shu, J.; Court, M.H.; Sun, Z.; Jiang, L.; Zheng, C.; Shu, H.; Ji, L.; et al. Genome-wide analysis of the apple family 1 glycosyltransferases identified a flavonoid-modifying UGT, MdUGT83L3, which is targeted by MdMYB88 and contributes to stress adaptation. *Plant Sci.* **2022**, *321*, 111314. [\[CrossRef\]](#) [\[PubMed\]](#)
50. Gan, Y.; Yu, B.; Liu, R.; Shu, B.; Liang, Y.; Zhao, Y.; Qiu, Z.; Yan, S.; Cao, B. Systematic analysis of the UDP-glucosyltransferase family: Discovery of a member involved in rutin biosynthesis in *Solanum melongena*. *Front. Plant Sci.* **2023**, *14*, 1310080. [\[CrossRef\]](#)
51. Mamoon, R.H.; Amjad, N.M.; Bao, L.; Hussain, S.Z.; Lee, J.M.; Ahmad, M.Q.; Chung, G.; Yang, S.H. Genome-wide analysis of Family-1 UDP-glycosyltransferases in soybean confirms their abundance and varied expression during seed development. *J. Plant Physiol.* **2016**, *206*, 87–97. [\[CrossRef\]](#)
52. Zhang, J.; Lin, L.M.; Cheng, W.W.; Song, X.; Long, Y.H.; Xing, Z.B. Genome-wide identification and expression analysis of glycosyltransferase gene family 1 in *Quercus robur* L. *J. Appl. Genet.* **2021**, *62*, 559–570. [\[CrossRef\]](#) [\[PubMed\]](#)
53. Rehman, H.M.; Nawaz, M.A.; Shah, Z.H.; Ludwig-Muller, J.; Chung, G.; Ahmad, M.Q.; Yang, S.H.; Lee, S.I. Comparative genomic and transcriptomic analyses of Family-1 UDP glycosyltransferase in three *Brassica* species and *Arabidopsis* indicates stress-responsive regulation. *Sci. Rep.* **2018**, *8*, 1875. [\[CrossRef\]](#) [\[PubMed\]](#)
54. Dong, L.; Tang, Z.; Yang, T.; Hao, F.; Deng, X. Genome-Wide Analysis of UGT Genes in *Petunia* and Identification of PhUGT51 Involved in the Regulation of Salt Resistance. *Plants* **2022**, *11*, 2434. [\[CrossRef\]](#)
55. Zhang, Z.; Zhuo, X.; Yan, X.; Zhang, Q. Comparative Genomic and Transcriptomic Analyses of Family-1 UDP Glycosyltransferase in *Prunus Mume*. *Int. J. Mol. Sci.* **2018**, *19*, 3382. [\[CrossRef\]](#)
56. Liao, J.H.; Chen, S.; Liu, D.; Zhang, J.J.; Liu, Y.F. Identification and expression of genome of uridine diphosphate glycosyltransferase (UGT) gene family from *Chrysanthemum indicum*. *Zhongguo Zhong Yao Za Zhi* **2024**, *49*, 702–716. [\[CrossRef\]](#)
57. Duan, Z.; Yan, Q.; Wu, F.; Wang, Y.; Wang, S.; Zong, X.; Zhou, P.; Zhang, J. Genome-Wide Analysis of the UDP-Glycosyltransferase Family Reveals Its Roles in Coumarin Biosynthesis and Abiotic Stress in *Melilotus albus*. *Int. J. Mol. Sci.* **2021**, *22*, 10826. [\[CrossRef\]](#) [\[PubMed\]](#)
58. Cheng, X.; Muhammad, A.; Li, G.; Zhang, J.; Cheng, J.; Qiu, J.; Jiang, T.; Jin, Q.; Cai, Y.; Lin, Y. Family-1 UDP glycosyltransferases in pear (*Pyrus bretschneideri*): Molecular identification, phylogenomic characterization and expression profiling during stone cell formation. *Mol. Biol. Rep.* **2019**, *46*, 2153–2175. [\[CrossRef\]](#)
59. Yu, A.; Jiang, X.; Sun, Y.; Hu, Q.; Zhu, X.; Kang, J.; Chen, L.; Liu, L.; Hao, L.; Yang, Q.; et al. Genome-wide identification, characterization, and expression analysis of UDP-glycosyltransferase genes associated with secondary metabolism in alfalfa (*Medicago sativa* L.). *Front. Plant Sci.* **2022**, *13*, 1001206. [\[CrossRef\]](#)

60. Wu, B.; Gao, L.; Gao, J.; Xu, Y.; Liu, H.; Cao, X.; Zhang, B.; Chen, K. Genome-Wide Identification, Expression Patterns, and Functional Analysis of UDP Glycosyltransferase Family in Peach (*Prunus persica* L. Batsch). *Front. Plant Sci.* **2017**, *8*, 389. [\[CrossRef\]](#)
61. Khorolragchaa, A.; Kim, Y.J.; Rahimi, S.; Sukweenadhi, J.; Jang, M.G.; Yang, D.C. Grouping and characterization of putative glycosyltransferase genes from *Panax ginseng* Meyer. *Gene* **2014**, *536*, 186–192. [\[CrossRef\]](#) [\[PubMed\]](#)
62. Zhou, M.; Fan, J.; Gao, Y.; Zheng, C.; Xu, Y.; Jia, L.; An, X.; Chen, Z. Identification and analysis of UGT genes associated with triterpenoid saponin in soapberry (*Sapindus mukorossi* Gaertn.). *BMC Plant Biol.* **2024**, *24*, 588. [\[CrossRef\]](#)
63. Chen, J.D.; Jiang, W.; Song, M.Q.; Zhou, Y.J.; Li, Y.P.; Duan, X.J.; Tao, Z.M. Identification and expression analysis of UDP-glycosyltransferase (UGT) gene family in *Dendrobium officinale*. *China J. Chin. Mater. Medica* **2023**, *48*, 1840–1850. (In Chinese) [\[CrossRef\]](#)
64. Yonekura-Sakakibara, K.; Fukushima, A.; Nakabayashi, R.; Hanada, K.; Matsuda, F.; Sugawara, S.; Inoue, E.; Kuromori, T.; Ito, T.; Shinozaki, K.; et al. Two glycosyltransferases involved in anthocyanin modification delineated by transcriptome independent component analysis in *Arabidopsis thaliana*. *Plant J.* **2012**, *69*, 154–167. [\[CrossRef\]](#)
65. Lim, E.K.; Bowles, D.J. A class of plant glycosyltransferases involved in cellular homeostasis. *Embo J.* **2004**, *23*, 2915–2922. [\[CrossRef\]](#)
66. Lin, J.S.; Huang, X.X.; Li, Q.; Cao, Y.; Bao, Y.; Meng, X.F.; Li, Y.J.; Fu, C.; Hou, B.K. UDP-glycosyltransferase 72B1 catalyzes the glucose conjugation of monolignols and is essential for the normal cell wall lignification in *Arabidopsis thaliana*. *Plant J.* **2016**, *88*, 26–42. [\[CrossRef\]](#)
67. Rehman, H.M.; Khan, U.M.; Nawaz, S.; Saleem, F.; Ahmed, N.; Rana, I.A.; Atif, R.M.; Shaheen, N.; Seo, H. Genome Wide Analysis of Family-1 UDP Glycosyltransferases in *Populus trichocarpa* Specifies Abiotic Stress Responsive Glycosylation Mechanisms. *Genes* **2022**, *13*, 1640. [\[CrossRef\]](#) [\[PubMed\]](#)
68. Krishnamurthy, P.; Tsukamoto, C.; Ishimoto, M. Reconstruction of the Evolutionary Histories of UGT Gene Superfamily in Legumes Clarifies the Functional Divergence of Duplicates in Specialized Metabolism. *Int. J. Mol. Sci.* **2020**, *21*, 1855. [\[CrossRef\]](#) [\[PubMed\]](#)
69. Su, K.; Wu, Z.; Liu, Y.; Wang, Y.; Wang, H.; Liu, M.; Wang, Y.; Wang, H.; Fu, C. UDP-glycosyltransferase UGT96C10 functions as a novel detoxification factor for conjugating the activated dinitrotoluene sulfonate in switchgrass. *Plant Biotechnol. J.* **2024**, *22*, 2530–2540. [\[CrossRef\]](#)
70. Kumar, R.; Sangwan, R.S.; Mishra, S.; Sabir, F.; Sangwan, N.S. In silico motif diversity analysis of the glycon preferentiality of plant secondary metabolic glycosyltransferases. *Plant Omics* **2012**, *5*, 200–210.
71. Yao, Y. Cloning and Functional Study of Glycosyltransferase UGT79 Family Genes from *Epimedium Pubescens*. PhD Thesis, Peking Union Medical College, Beijing, China, 2023. (In Chinese).
72. Zhang, F.; Guo, H.; Huang, J.; Yang, C.; Li, Y.; Wang, X.; Qu, L.; Liu, X.; Luo, J. A UV-B-responsive glycosyltransferase, OsUGT706C2, modulates flavonoid metabolism in rice. *Sci. China Life Sci.* **2020**, *63*, 1037–1052. [\[CrossRef\]](#)
73. Irmisch, S.; Jancsik, S.; Man, S.Y.M.; Madilao, L.L.; Bohlmann, J. Complete Biosynthesis of the Anti-Diabetic Plant Metabolite Montbretin A. *Plant Physiol.* **2020**, *184*, 97–109. [\[CrossRef\]](#)
74. Li, Y.; Baldauf, S.; Lim, E.K.; Bowles, D.J. Phylogenetic analysis of the UDP-glycosyltransferase multigene family of *Arabidopsis thaliana*. *J. Biol. Chem.* **2001**, *276*, 4338–4343. [\[CrossRef\]](#)
75. Chen, H.Y.; Li, X. Identification of a residue responsible for UDP-sugar donor selectivity of a dihydroxybenzoic acid glycosyltransferase from *Arabidopsis* natural accessions. *Plant J.* **2017**, *89*, 195–203. [\[CrossRef\]](#) [\[PubMed\]](#)
76. Chen, Q.; Jiang, L.Y.; Wang, Y.; Zhang, Y.T.; Wang, X.R.; Tang, H.R. Isolation, identification of blackberry glycosyltransferase gene UGT78H2 and molecular docking with flavonoids. *Bull. Bot. Res.* **2015**, *35*, 270–278. (In Chinese)
77. Yao, Y.; Gu, J.J.; Sun, C.; Shen, G.A.; Guo, B.L. Research progress on plant flavonoid UDP-glycosyltransferases. *Biotechnol. Bull.* **2022**, *38*, 47–57. (In Chinese) [\[CrossRef\]](#)
78. Zhao, C.X.; Yan, Y.F.; Zhao, L.X.; Tang, X.; Chen, Y.G.; Song, W.J.; Long, L.P.; Chen, J.; Tan, C.L.; Zhang, Q.Z.; et al. Characterization of a 4'-O-rhamnosyltransferase and de novo biosynthesis of bioactive steroidal triglycosides from *Paris polyphylla*. *Plant Commun.* **2025**, *6*, 101257. [\[CrossRef\]](#)
79. Zhou, Y.; Li, W.; You, W.; Di, Z.; Wang, M.; Zhou, H.; Yuan, S.; Wong, N.K.; Xiao, Y. Discovery of *Arabidopsis* UGT73C1 as a steviol-catalyzing UDP-glycosyltransferase with chemical probes. *Chem. Commun.* **2018**, *54*, 7179–7182. [\[CrossRef\]](#) [\[PubMed\]](#)
80. Huang, X.X.; Wang, Y.; Lin, J.S.; Chen, L.; Li, Y.J.; Liu, Q.; Wang, G.F.; Xu, F.; Liu, L.; Hou, B.K. The novel pathogen-responsive glycosyltransferase UGT73C7 mediates the redirection of phenylpropanoid metabolism and promotes SNC1-dependent *Arabidopsis* immunity. *Plant J.* **2021**, *107*, 149–165. [\[CrossRef\]](#)
81. Yonekura-Sakakibara, K.; Hanada, K. An evolutionary view of functional diversity in family 1 glycosyltransferases. *Plant J.* **2011**, *66*, 182–193. [\[CrossRef\]](#)
82. Hou, B.; Lim, E.K.; Higgins, G.S.; Bowles, D.J. N-glucosylation of cytokinins by glycosyltransferases of *Arabidopsis thaliana*. *J. Biol. Chem.* **2004**, *279*, 47822–47832. [\[CrossRef\]](#) [\[PubMed\]](#)

83. Ohgami, S.; Ono, E.; Toyonaga, H.; Watanabe, N.; Ohnishi, T. Identification and characterization of *Camellia sinensis* glucosyltransferase, UGT73A17: A possible role in flavonol glucosylation. *Plant Biotechnol-Nar.* **2014**, *31*, 573–578. [[CrossRef](#)]
84. Behr, M.; Neutelings, G.; El, J.M.; Baucher, M. You Want it Sweeter: How Glycosylation Affects Plant Response to Oxidative Stress. *Front. Plant Sci.* **2020**, *11*, 571399. [[CrossRef](#)]
85. Yin, Q.; Shen, G.; Di, S.; Fan, C.; Chang, Z.; Pang, Y. Genome-Wide Identification and Functional Characterization of UDP-Glucosyltransferase Genes Involved in Flavonoid Biosynthesis in *Glycine max*. *Plant Cell Physiol.* **2017**, *58*, 1558–1572. [[CrossRef](#)] [[PubMed](#)]
86. Huang, J.; Li, J.; Yue, J.; Huang, Z.; Zhang, L.; Yao, W.; Guan, R.; Wu, J.; Liang, J.; Duan, L.; et al. Functional Characterization of a Novel Glycosyltransferase (UGT73CD1) from *Iris tectorum* Maxim. for the Substrate promiscuity. *Mol. Biotechnol.* **2021**, *63*, 1030–1039. [[CrossRef](#)]
87. Seki, H.; Tamura, K.; Muranaka, T. P450s and UGTs: Key Players in the Structural Diversity of Triterpenoid Saponins. *Plant Cell Physiol.* **2015**, *56*, 1463–1471. [[CrossRef](#)]
88. Hwang, H.S.; Lee, H.; Choi, Y.E. Transcriptomic analysis of Siberian Ginseng (*Eleutherococcus senticosus*) to discover genes involved in saponin biosynthesis. *BMC Genom.* **2015**, *16*, 180. [[CrossRef](#)]
89. Yu, X.; Yu, J.; Liu, S.; Liu, M.; Wang, K.; Zhao, M.; Wang, Y.; Chen, P.; Lei, J.; Wang, Y.; et al. Transcriptome-Wide Identification and Integrated Analysis of a UGT Gene Involved in Ginsenoside Ro Biosynthesis in *Panax ginseng*. *Plants* **2024**, *13*, 604. [[CrossRef](#)]
90. Khakimov, B.; Kuzina, V.; Erthmann, P.O.; Fukushima, E.O.; Augustin, J.M.; Olsen, C.E.; Scholtalbers, J.; Volpin, H.; Andersen, S.B.; Hauser, T.P.; et al. Identification and genome organization of saponin pathway genes from a wild crucifer, and their use for transient production of saponins in *Nicotiana benthamiana*. *Plant J.* **2015**, *84*, 478–490. [[CrossRef](#)]
91. Jones, P.; Messner, B.; Nakajima, J.; Schaffner, A.R.; Saito, K. UGT73C6 and UGT78D1, glycosyltransferases involved in flavonol glycoside biosynthesis in *Arabidopsis thaliana*. *J. Biol. Chem.* **2003**, *278*, 43910–43918. [[CrossRef](#)] [[PubMed](#)]
92. Bao, H.; Yuan, L.; Luo, Y.; Jing, X.; Zhang, Z.; Wang, J.; Zhu, G. A freezing responsive UDP-glycosyltransferase improves potato freezing tolerance via modifying flavonoid metabolism. *Hortic. Plant J.* **2025**, *11*, 1595–1606. [[CrossRef](#)]
93. Song, C.; Zhao, S.; Hong, X.; Liu, J.; Schulenburg, K.; Schwab, W. A UDP-glucosyltransferase functions in both acylphloroglucinol glucoside and anthocyanin biosynthesis in strawberry (*Fragaria × ananassa*). *Plant J.* **2016**, *85*, 730–742. [[CrossRef](#)]
94. Li, H.; Ma, W.; Lyv, Y.; Gao, S.; Zhou, J. Glycosylation Modification Enhances (2S)-Naringenin Production in *Saccharomyces cerevisiae*. *ACS Synth. Biol.* **2022**, *11*, 2339–2347. [[CrossRef](#)] [[PubMed](#)]
95. Su, X.; Wang, W.; Xia, T.; Gao, L.; Shen, G.; Pang, Y. Characterization of a heat responsive UDP: Flavonoid glucosyltransferase gene in tea plant (*Camellia sinensis*). *PLoS ONE* **2018**, *13*, e0207212. [[CrossRef](#)]
96. Wang, S.; Sun, S.; Du, Z.; Gao, F.; Li, Y.; Han, W.; Wu, R.; Yu, X. Characterization of CsUGT73AC15 as a Multifunctional Glycosyltransferase Impacting Flavonol Triglycoside Biosynthesis in Tea Plants. *J. Agric. Food Chem.* **2024**, *72*, 13328–13340. [[CrossRef](#)]
97. Liu, X.; Xu, W.; Li, J.; Feng, X.; Li, C. Identification of a permissive glycosyltransferase UGT73AC11 for flavonoids glycosylation. *Biochem. Eng. J.* **2024**, *209*, 109372. [[CrossRef](#)]
98. Yin, Q.; Han, X.; Chen, J.; Han, Z.; Shen, L.; Sun, W.; Chen, S. Identification of Specific Glycosyltransferases Involved in Flavonol Glucoside Biosynthesis in Ginseng Using Integrative Metabolite Profiles, DIA Proteomics, and Phylogenetic Analysis. *J. Agric. Food Chem.* **2021**, *69*, 1714–1726. [[CrossRef](#)]
99. Xu, B.; Huang, J.P.; Peng, G.; Cao, W.; Liu, Z.; Chen, Y.; Yao, J.; Wang, Y.J.; Li, J.; Zhang, G.; et al. Total biosynthesis of the medicinal triterpenoid saponin astragalosides. *Nat. Plants* **2024**, *10*, 1826–1837. [[CrossRef](#)] [[PubMed](#)]
100. Zhong, Y.; Xue, X.; Liu, Z.; Ma, Y.; Zeng, K.; Han, L.; Qi, J.; Ro, D.K.; Bak, S.; Huang, S.; et al. Developmentally Regulated Glucosylation of Bitter Triterpenoid in Cucumber by the UDP-Glucosyltransferase UGT73AM3. *Mol. Plant* **2017**, *10*, 1000–1003. [[CrossRef](#)]
101. Louveau, T.; Orme, A.; Pfalzgraf, H.; Stephenson, M.J.; Melton, R.; Saalbach, G.; Hemmings, A.M.; Leveau, A.; Rejzek, M.; Vickerstaff, R.J.; et al. Analysis of Two New Arabinosyltransferases Belonging to the Carbohydrate-Active Enzyme (CAZY) Glycosyl Transferase Family1 Provides Insights into Disease Resistance and Sugar Donor Specificity. *Plant Cell* **2018**, *30*, 3038–3057. [[CrossRef](#)]
102. Liu, X.; Zhang, L.; Feng, X.; Lv, B.; Li, C. Biosynthesis of Glycyrrhetic Acid-3-O-monoglucose Using Glycosyltransferase UGT73C11 from *Barbarea vulgaris*. *Ind. Eng. Chem. Res.* **2017**, *56*, 14949–14958. [[CrossRef](#)]
103. Kim, O.T.; Jin, M.L.; Lee, D.Y.; Jetter, R. Characterization of the Asiatic Acid Glucosyltransferase, UGT73AH1, Involved in Asiaticoside Biosynthesis in *Centella asiatica* (L.) Urban. *Int. J. Mol. Sci.* **2017**, *18*, 2630. [[CrossRef](#)]
104. He, J.; Chen, K.; Hu, Z.M.; Li, K.; Song, W.; Yu, L.Y.; Leung, C.H.; Ma, D.L.; Qiao, X.; Ye, M. UGT73F17, a new glycosyltransferase from *Glycyrrhiza uralensis*, catalyzes the regiospecific glycosylation of pentacyclic triterpenoids. *Chem. Commun.* **2018**, *54*, 8594–8597. [[CrossRef](#)]
105. Zhang, L.; Ren, S.; Liu, X.; Liu, X.; Guo, F.; Sun, W.; Feng, X.; Li, C. Mining of UDP-glucosyltransferases in licorice for controllable glycosylation of pentacyclic triterpenoids. *Biotechnol. Bioeng.* **2020**, *117*, 3651–3663. [[CrossRef](#)] [[PubMed](#)]

106. Li, J.; Chen, T.; Zhang, X.; Yang, J.; Zeng, Y.; Men, Y.; Sun, Y. Multienzyme Synthesis of Glycyrrhetic Acid 3-O-mono- β -d-glucuronide by Coupling UGT73F15 to UDP-Glucuronic Acid Regeneration Module. *Catalysts* **2023**, *13*, 104. [\[CrossRef\]](#)
107. Wang, Y.; Zhang, H.; Ri, H.C.; An, Z.; Wang, X.; Zhou, J.N.; Zheng, D.; Wu, H.; Wang, P.; Yang, J.; et al. Deletion and tandem duplications of biosynthetic genes drive the diversity of triterpenoids in *Aralia elata*. *Nat. Commun.* **2022**, *13*, 2224. [\[CrossRef\]](#)
108. Naoumkina, M.A.; Modolo, L.V.; Huhman, D.V.; Urbanczyk-Wochniak, E.; Tang, Y.; Sumner, L.W.; Dixon, R.A. Genomic and coexpression analyses predict multiple genes involved in triterpene saponin biosynthesis in *Medicago truncatula*. *Plant Cell* **2010**, *22*, 850–866. [\[CrossRef\]](#)
109. Poppenberger, B.; Berthiller, F.; Lucyshyn, D.; Sieberer, T.; Schuhmacher, R.; Krska, R.; Kuchler, K.; Glossl, J.; Luschign, C.; Adam, G. Detoxification of the Fusarium mycotoxin deoxynivalenol by a UDP-glucosyltransferase from *Arabidopsis thaliana*. *J. Biol. Chem.* **2003**, *278*, 47905–47914. [\[CrossRef\]](#)
110. Gandia-Herrero, F.; Lorenz, A.; Larson, T.; Graham, I.A.; Bowles, D.J.; Rylott, E.L.; Bruce, N.C. Detoxification of the explosive 2,4,6-trinitrotoluene in *Arabidopsis*: Discovery of bifunctional O- and C-glucosyltransferases. *Plant J.* **2008**, *56*, 963–974. [\[CrossRef\]](#)
111. Langlois-Meurinne, M.; Gachon, C.M.; Saindrenan, P. Pathogen-responsive expression of glucosyltransferase genes *UGT73B3* and *UGT73B5* is necessary for resistance to *Pseudomonas syringae* pv *tomato* in *Arabidopsis*. *Plant Physiol.* **2005**, *139*, 1890–1901. [\[CrossRef\]](#) [\[PubMed\]](#)
112. Simon, C.; Langlois-Meurinne, M.; Didierlaurent, L.; Chaouch, S.; Bellvert, F.; Massoud, K.; Garmier, M.; Thareau, V.; Comte, G.; Noctor, G.; et al. The secondary metabolism glucosyltransferases *UGT73B3* and *UGT73B5* are components of redox status in resistance of *Arabidopsis* to *Pseudomonas syringae* pv. *tomato*. *Plant Cell Environ.* **2014**, *37*, 1114–1129. [\[CrossRef\]](#)
113. Zhang, D.; Li, X.; Bei, F.; Jin, T.; Jia, S.; Bu, R.; Wang, J.; Wang, H.; Liu, W. Investigating the Metabolic Mesosulfuron-Methyl Resistance in *Aegilops tauschii* Coss. By Transcriptome Sequencing Combined with the Reference Genome. *J. Agric. Food Chem.* **2022**, *70*, 11429–11440. [\[CrossRef\]](#)
114. Brazier-Hicks, M.; Gershtater, M.; Dixon, D.; Edwards, R. Substrate specificity and safener inducibility of the plant UDP-glucose-dependent family 1 glucosyltransferase super-family. *Plant Biotechnol. J.* **2018**, *16*, 337–348. [\[CrossRef\]](#) [\[PubMed\]](#)
115. Franco-Ortega, S.; Goldberg-Cavalleri, A.; Walker, A.; Brazier-Hicks, M.; Onkokesung, N.; Edwards, R. Non-target Site Herbicide Resistance Is Conferred by Two Distinct Mechanisms in Black-Grass (*Alopecurus myosuroides*). *Front. Plant Sci.* **2021**, *12*, 636652. [\[CrossRef\]](#)
116. Landa, P.; Prerostova, S.; Langhansova, L.; Marsik, P.; Vanek, T. Transcriptomic response of *Arabidopsis thaliana* L. Heynh. roots to ibuprofen. *Int. J. Phytoremediat.* **2017**, *19*, 695–700. [\[CrossRef\]](#) [\[PubMed\]](#)
117. Yu, H.S.; Ma, L.Q.; Zhang, J.X.; Shi, G.L.; Hu, Y.H.; Wang, Y.N. Characterization of glucosyltransferases responsible for salidroside biosynthesis in *Rhodiola sachalinensis*. *Phytochemistry* **2011**, *72*, 862–870. [\[CrossRef\]](#) [\[PubMed\]](#)
118. Chen, Y.; Yan, Q.; Ji, Y.; Bai, X.; Li, D.; Mu, R.; Guo, K.; Yang, M.; Tao, Y.; Gershenzon, J.; et al. Unraveling the serial glycosylation in the biosynthesis of steroidal saponins in the medicinal plant *Paris polyphylla* and their antifungal action. *Acta Pharm. Sin. B* **2023**, *13*, 4638–4654. [\[CrossRef\]](#)
119. Sun, G.; Strebl, M.; Merz, M.; Blamberg, R.; Huang, F.C.; Mcgrathery, K.; Hoffmann, T.; Schwab, W. Glucosylation of the phytoalexin N-feruloyl tyramine modulates the levels of pathogen-responsive metabolites in *Nicotiana benthamiana*. *Plant J.* **2019**, *100*, 20–37. [\[CrossRef\]](#)
120. Di, S.K.; Yin, Q.G.; Xia, Y.Y.; Pang, Y.Z. Functional study of soybean flavonoid glucosyltransferase gene *UGT73C19*. *Sci. Agric. Sin.* **2019**, *52*, 3507–3519. (In Chinese)
121. Erthmann, P.O.; Agerbirk, N.; Bak, S. A tandem array of UDP-glucosyltransferases from the UGT73C subfamily glycosylate sapogenins, forming a spectrum of mono- and bisdesmosidic saponins. *Plant Mol. Biol.* **2018**, *97*, 37–55. [\[CrossRef\]](#)
122. de Costa, F.; Barber, C.; Kim, Y.B.; Reed, D.W.; Zhang, H.; Fett-Neto, A.G.; Covello, P.S. Molecular cloning of an ester-forming triterpenoid: UDP-glucose 28-O-glucosyltransferase involved in saponin biosynthesis from the medicinal plant *Centella asiatica*. *Plant Sci.* **2017**, *262*, 9–17. [\[CrossRef\]](#)
123. Lim, E.K.; Doucet, C.J.; Li, Y.; Elias, L.; Worrall, D.; Spencer, S.P.; Ross, J.; Bowles, D.J. The activity of *Arabidopsis* glucosyltransferases toward salicylic acid, 4-hydroxybenzoic acid, and other benzoates. *J. Biol. Chem.* **2002**, *277*, 586–592. [\[CrossRef\]](#)
124. Gao, Y.; Zhang, L.; Feng, X.; Liu, X.; Guo, F.; Lv, B.; Li, C. Galactosylation of Monosaccharide Derivatives of Glycyrrhetic Acid by UDP-Glycosyltransferase GmSGT2 from *Glycine max*. *J. Agric. Food Chem.* **2020**, *68*, 8580–8588. [\[CrossRef\]](#)
125. Wang, M.; Ji, Q.; Lai, B.; Liu, Y.; Mei, K. Structure-function and engineering of plant UDP-glucosyltransferase. *Comput. Struct. Biotechnol. J.* **2023**, *21*, 5358–5371. [\[CrossRef\]](#)
126. Song, W.; Zhang, C.; Wu, J.; Qi, J.; Hua, X.; Kang, L.; Yuan, Q.; Yuan, J.; Xue, Z. Characterization of Three *Paris polyphylla* Glucosyltransferases from Different UGT Families for Steroid Functionalization. *ACS Synth. Biol.* **2022**, *11*, 1669–1680. [\[CrossRef\]](#) [\[PubMed\]](#)
127. Forrester, T.; Ovchinnikova, O.G.; Li, Z.; Kitova, E.N.; Nothof, J.T.; Koizumi, A.; Klassen, J.S.; Lowary, T.L.; Whitfield, C.; Kimber, M.S. The retaining beta-Kdo glucosyltransferase WbbB uses a double-displacement mechanism with an intermediate adduct rearrangement step. *Nat. Commun.* **2022**, *13*, 6277. [\[CrossRef\]](#)

128. Aykut, A.O.; Atilgan, A.R.; Atilgan, C. Designing molecular dynamics simulations to shift populations of the conformational states of calmodulin. *PLoS Comput. Biol.* **2013**, *9*, e1003366. [[CrossRef](#)] [[PubMed](#)]
129. Fan, Z.; Tieman, D.M.; Knapp, S.J.; Zerbe, P.; Famula, R.; Barbey, C.R.; Folta, K.M.; Amadeu, R.R.; Lee, M.; Oh, Y.; et al. A multi-omics framework reveals strawberry flavor genes and their regulatory elements. *New Phytol.* **2022**, *236*, 1089–1107. [[CrossRef](#)]
130. Gilbert, M.K.; Bland, J.M.; Shockey, J.M.; Cao, H.; Hinchliffe, D.J.; Fang, D.D.; Naoumkina, M. A transcript profiling approach reveals an abscisic acid-specific glycosyltransferase (UGT73C14) induced in developing fiber of *Ligon lintless-2* mutant of cotton (*Gossypium hirsutum* L.). *PLoS ONE* **2013**, *8*, e75268. [[CrossRef](#)] [[PubMed](#)]
131. Jin, Y.; Yan, H.; Zhu, X.; Yang, Y.; Jia, J.; Sun, M.; Najeeb, A.; Luo, J.; Wang, X.; He, M.; et al. Single-cell transcriptomes reveal spatiotemporal heat stress response in pearl millet leaves. *New Phytol.* **2025**, *247*, 637–650. [[CrossRef](#)]
132. Lu, M.; Guo, J.; Dong, D.; Zhang, M.; Li, Q.; Cao, Y.; Dong, Y.; Chen, C.; Jin, X. UDP-glycosyltransferase gene SIUGT73C1 from *Solanum lycopersicum* regulates salt and drought tolerance in *Arabidopsis thaliana* L. *Funct. Integr. Genom.* **2023**, *23*, 320. [[CrossRef](#)]
133. Ouyang, L. Functional Study of Flavonoid Glycosyltransferase AhUGT75A in Regulating Stress Resistance of Peanut. Master's Thesis, Hubei University, Wuhan, China, 2024. (In Chinese)
134. Qian, P.P. Functional Analysis of Soybean Glycosyltransferases UGT73F2 and UGT73F4 Involved in Plant Tolerance to Abiotic Stress. Master's Thesis, Nanjing Agricultural University, Nanjing, China, 2019. (In Chinese)
135. Haoran Ren, Y.L.M.O. Integrated metabolomic and transcriptomic profiling reveals the key role of UDP-glycosyltransferase 73D1 (UGT73D1) in rose under UV-B irradiation. *Hortic. Plant J.* **2025**. [[CrossRef](#)]
136. Cheng, W.; Fang, X.; Guan, Z.; Yao, Y.; Xu, Z.; Bi, Y.; Ren, K.; Li, J.; Chen, F.; Chen, X.; et al. Functional characterization and structural basis of a reversible glycosyltransferase involves in plant chemical defence. *Plant Biotechnol. J.* **2023**, *21*, 2611–2624. [[CrossRef](#)]
137. Zhang, T.; Tian, S.; Gao, Z.; Li, Y.; Jia, H. Engineering an Ancestral Glycosyltransferase for Biosynthesis of 2-Phenylethyl-beta-d-Glucopyranoside and Salidroside. *J. Agric. Food Chem.* **2024**, *72*, 19966–19976. [[CrossRef](#)]
138. Chen, X.; Ma, Y.; Huang, M.; Li, W.; Zeng, D.; Li, J.; Wang, Y. Multiple herbicide resistance in a *Cyperus difformis* population in rice field from China. *Pestic. Biochem. Phys.* **2023**, *195*, 105576. [[CrossRef](#)] [[PubMed](#)]
139. Ma, H.; Chen, J.; Lin, F.; Fan, H.; Zhang, T.; Zhang, S.; Cheng, S.; Xin, P.; Chu, J.; Chai, T.; et al. Functional Characterization of PcUGT73BF6 from Polygonum Cuspidatum and the Facilitation of Emodin Catalysis via Site-Directed Mutagenesis. *J. Agric. Food Chem.* **2025**, *73*, 13540–13554. [[CrossRef](#)] [[PubMed](#)]
140. Lu, X.; Li, J.; Huang, C.; Wang, Z.; Chen, Y.; Jiang, S.; Li, J.; Xie, N. Development of New Multi-Glycosylation Routes to Facilitate the Biosynthesis of Sweetener Mogrosides from Bitter Immature *Siraitia Grosvenorii* Using Engineered *Escherichia coli*. *J. Agr. Food Chem.* **2024**, *72*, 18078–18088. [[CrossRef](#)]
141. Wang, J.; Wang, Z.; Wang, H.; Pai, M.; Li, T.; Zhang, H.; Ye, B.; Tang, L.; Fu, R.; Zhang, Y. UDP-glucosyltransferases from UGT73 family catalyze 3-O-glucosylation of isosteroidal and steroidal alkaloids in *Fritillaria unibracteata* var. *wabuensis*. *Plant J.* **2025**, *121*, e70042. [[CrossRef](#)]
142. Chen, N.; Jiang, Z.; Xie, Z.; Zhou, S.; Zeng, T.; Jiang, S.; Zheng, Y.; Yuan, Y.; Wu, R. An Effective Computational Strategy for UGTs Catalytic Function Prediction. *ACS Synth. Biol.* **2025**, *14*, 2064–2080. [[CrossRef](#)] [[PubMed](#)]

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