



Mini Review

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Functional Aspects of Plant Uridine Diphosphate Glycosyltransferase



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Abstract

Glycosyltransferases (GTs; EC2.4.x.y) are a family of multi member transferases that can catalyze the formation of glycosidic bonds between specific sugars and receptors. GTs take different sugar groups as donors, catalyze the transfer of sugar molecules to acceptor molecules, and can regulate the physicochemical properties of acceptor molecules and thus regulate their biological activities. Thus, GTs play an important role in glycosylation modification of secondary metabolites, detoxification of endogenous or exogenous substances, body defense and hormone regulation. Plant uridine diphosphate glycosyltransferase (UGT) belongs to the glycosyltransferase family 1. It mainly uses the most common uridine diphosphate (UDP) - sugars in plants as activated glycosyl molecule donors, and small molecule compounds such as Due to the wide variety of substrates catalyzed by UGT and the large difference in product activities, the glycosylation reaction catalyzed by UGT plays a very important role in plant growth, development and metabolic regulation. In this paper, the functional roles of plant UGT family in plant secondary metabolism, hormone regulation and stress response were summarized, aiming to provide some references for the functional studies and application prospects of plant UGT.

Keywords: Uridine diphosphate Glycosyltransferase; Glycosylation; Secondary metabolite; hormone regulation; Stress

Introduction

Glycosyltransferases (GTs; EC2.4.x.y), which are present in almost all organisms, catalyze the transfer of sugar moieties from an activated donor molecule to an acceptor molecule, and are one of the most important biotransformation reactions, directly involved in the biosynthesis of disaccharides, monosaccharides, oligosaccharides, polyglycosides, and polysaccharides [1]. Glycosyl donor molecules include disaccharides or polysaccharides, 1-phosphate sugars, nucleoside-2-phosphate sugars, uridine diphosphate glucuronic acid [2]. The most common glycosyl donor in plants is uridine diphosphate (UDP) glucose, in addition to UDP galactose, UDP rhamnose, UDP xylose and UDP glucuronic acid [3]. Common glycosyl receptors include, in addition to monosaccharides, oligosaccharides, and polysaccharides, noncarbohydrates such as proteins, lipids, antibiotics, sterols, phenolics, terpenes, cyanohydrins, phytohormones, alkaloids, phytotoxins, and xenobiotics (e.g., insecticidal agents), among others [3-5]. Glycosylation can change the hydrophilicity, chemical stability, biological activity and subcellular localization of receptor

molecules, which is helpful for their transportation and storage in cells and organisms [3,6].

GTs are divided into 110 different families, based on amino acid sequence similarity, substrate specificity, and catalytic specificity (Carbohydrate Active enzymes Database, CAZy, <http://www.cazy.org>), among which glycosyltransferase family 1 (GT1) has the largest number of members and the most important function. The GT1 family is often called UDP glycosyltransferase (UGT), because it mainly catalyzes the transfer of UDP sugars to specific receptors such as proteins, nucleic acids, antibiotics, alkaloids and phytohormones, and can regulate plant signaling pathways and intracellular homeostasis with a wide range of roles [7]. At present, UGT family encoding genes in plants have been reported in several species, such as wheat, soybean, rice [8-10]. The mechanism of the action of UGT family encoding proteins on glycosylation reactions in the process of plant vegetative growth and reproductive growth and development also has a certain basis. This review focuses on recent biochemical and molecular insights

into UGT involved in the glycosylation of secondary metabolites, phytohormones and biological substances.

Characteristics of Plant UGT Family

The systematic classification of the GT superfamily is included in the cazy database (<http://www.cazy.org>). UGT belongs to the GT1 family, and its C-terminal contains a conserved sequence PspG box composed of 44 amino acids, which is considered to be the region that binds to UDP - sugar donors [2]. UGT, as a superfamily, is classified and named according to the system established by GT Nomenclature Committee. The Arabic numbers behind UGT indicate families, where 1 - 50 are of animal origin UGTs, 51 - 70 are of yeast origin, 71 - 100 are of plant origin, and 101 - 200 are of bacterial origin. Subsequently, letters after numbers indicate subfamilies, numbers after letters indicate gene family members [2]. There are 107 members of the UGT family in *Arabidopsis*, which have been classified into 14 phylogenetic groups, designated A - N based on sequence homology [6], and groups O, P, Q and R have subsequently been identified in plants such as *Populus trichocarpa*, grape, apple, tea and maize [11,12]. With 241 UGT family members, apple currently has the largest UGT family. In the evolution of higher plants, groups A, D, E, G, and L expanded faster; Groups D and E are the larger groups in plants [11].

Plant UGTs mainly use UDP sugars such as UDP glucose, UDP galactose, UDP rhamnose, and UDP xylose as donors to glycosylate receptor small molecule compounds such as flavonoids, phenolic acids, terpenes and phytohormones, thereby generating various sugars and glycoside compounds [13], participating in the synthesis, transportation and storage of plant secondary metabolites, and further regulating plant metabolic homeostasis [14]. In addition, the catalytic substrates of plant UGT are diverse, mainly depending on the specificity of cellular expression, the relative availability of substrates, and the relative compartmentalization characteristics of enzymes and substrates.

Plant UGTs involved in the Synthesis of Secondary Metabolites

There are many kinds of plant secondary metabolites with different structures, which are mainly divided into three categories: phenols, terpenes and nitrogen-containing organic compounds. There are thousands or even tens of thousands of known compounds in each class, for example, about 6000 flavonoids have been identified [15-17]. Some of these compounds are chemically modified, and glycosylation reaction is one of its important modification reactions [3]. Flavonoids are multifunctional polyphenols of great significance to plant, animal and human health, which effectively delay aging and have antioxidant, anti-inflammatory, and other effects in humans [18]. And plant UGT glycosylation modifies many flavonoid compounds, mainly by catalyzing different flavonoid glycosides such as flavonols, flavanols, flavanones, flavonoids,

isoflavones and anthocyanins in the cytoplasm to generate different flavonoid glycosides [19]. A previous study reported that UGT73C6 and UGT78D1 found in *Arabidopsis* have the catalytic function of generating flavonol glycosides [20]. More studies indicated that GmUGT72X4, GmUGT72Z3 and GmUGT92G4 of soybeans showed flavonol specific activities, GmUGT73C20 and GmUGT88E19 showed activities on both flavonols and isoflavone aglycones [21]. Rice GSA1 has glycosyltransferase activity toward flavonoid and lignol monomers [10]. It was also reported that a glycosyltransferase can catalyze both flavonols and anthocyanins to form the corresponding glycosides in *Vitis vinifera* [22].

Anthocyanins belong to flavonoids, which can give various colors to plant organs [23,24]. In the biosynthesis pathway of anthocyanins, glycosylation is often used as the final reaction of anthocyanin synthesis, which can reduce its reaction activity and improve its stability and transportability [25]. The study was reported that overexpression of AtUGT79B2 and AtUGT79B3 can significantly increase anthocyanin accumulation in *Arabidopsis* [26]. Terpenoids are the largest group of natural products with more than 40 000 structures, and have many important functions such as antitumor, antimicrobial, antimicrobial, hypoglycemic, antioxidant and antiparasitic activities [27,28]. Its glycosylation modification process is to catalyze the transfer of active nucleotide sugars to acceptor aglycones to form glycosides, so that lipophilic compounds can be converted into hydrophilic compounds, which is conducive to the accumulation, storage and transportation of hydrophobic substances [29]. At present, the studies on the glycosylation of terpenoids catalyzed by UGT, mainly focus on the terpenoids such as nerol, linalool, steviol and saponins [9,30-32]. Plant UGTs glycosylate a variety of terpenoids and are able to bring about changes in their corresponding aglycon contents and activities, which are beneficial to the improvement of the yield and quality of the target product.

Plant UGTs involved in Hormones

Generally, the reactions of plant free hormones to form bound state hormones are reversible, and thus such reactions are able to regulate hormone content levels in plants, and glycosylation reaction is one of the major binding reactions [33]. Plant UGTs can participate in the regulation of auxin glycosylation through multiple pathways and effectively maintain auxin homeostasis. The formation of auxin glucose conjugates is considered one of the molecular modifications that control auxin homeostasis. The glycosyltransferase AtUGT76F1 is able to glycosylate indole-3-pyruvic acid (IPyA), the synthetic precursor of indole-3-acetic acid (IAA), and generate IPyA glucose conjugates (IPyA-Glc), thereby regulating the light signal to maintain the auxin homeostasis of *Arabidopsis* [34]. The glycosyltransferase AtUGT84B1 can glycosylate IAA to IAA-glucoside, and also catalyze phenylacetic acid (PAA) to generate PAA-glucoside in vitro [35].

Plant UGTs will be induced by exogenous abscisic acid (ABA) to trigger changes in the expression of genes involved in its own

ABA synthesis and signaling pathway, to respond to glycosylation modification of ABA compounds, and ultimately to changes in ABA content and activity, which will have an impact on the biological processes of plant growth and development mediated by ABA. It was reported that the expression of AtUGT74F2 was significantly up-regulated under ABA treatment in *Arabidopsis* [36]. UGT can participate in the glycosylation of ABA, thus affecting the ABA signaling pathway, and directly change the content of ABA and ABA-glucoside [37]. CsUGT85A53 of *Camellia sinensis* generates inactive ABA-glucoside by glycosylating ABA in vitro and in vivo [38]. Cytokinins (CK) mainly exist in plants as glycosides, and their glycosylation modification is catalyzed by the GT1 family [39]. Identification and characterization of CK glycosyltransferases are helpful to improve and increase plant yield. Studies showed that *Arabidopsis* specific o-glycosyltransferases AtUGT76C1, AtUGT76C2 and AtUGT85A1 could glycosylate CK to inactivate it [40]. Moreover, rice glycosyltransferase OS6 is able to glycosylate CK in vitro [41].

Plants can maintain a stable level of salicylic acid (SA) by glycosylating SA or methylsalicylate (MeSA) to regulate the plant immune system and programmed cell death [13]. It was reported that the induction of glycosyltransferases AtUGT73B3 and AtUGT73B5, is partially dependent on SA in *Arabidopsis* [42]. AtUGT76D1 can glycosylate two breakdown products of SA, 2,3-dihydroxybenzoic acid (2,3-DHBA) and 2,5-dihydroxybenzoic acid (2,5-DHBA), to generate glucose and xylose conjugates in vitro and in vivo. Overexpression of this gene will increase the accumulation of SA and enhance its immune response ability [43]. Brassinosteroids (BR) are a class of plant specific sterol hormones, which can interact with hormones such as IAA, CK, and SA [44,45]. BR in catabolism, depending on the different location of the glycosylation modification, conjugates or can act as catabolites that are ultimately inactivated, or can be stored in a short-lived form, in the β - mobilized upon glucosidase activation [5]. The glycosyltransferase AtUGT73C can catalyze the 23-o-glycosylation of brassinolide (BL) leading to hormone inactivation in *Arabidopsis* [46]. Methyl jasmonate (MeJA) is a class of hormones involved in plant signaling, alleviating stress damage [47]. It was reported that AtJGT1 protein can catalyze the generation of a variety of glucose conjugates from substrates such as dihydrojasmonic acid, IAA, and IBA in *Arabidopsis* [48].

Plant UGTs involved in Stress Response to Adversity

Plant UGTs can synthesize and modify biological stress regulators and participate in regulating plant response to biological stress [49]. The study showed that AtUGT76B1 could catalyze the synthesis of 1-O-glucosyl-pyrrolic acid to modify N-hydroxyphenylacetic acid (NHP) in *Arabidopsis* in vitro, playing an important role in maintaining the balance between plant growth and defense responses [50]. Plant UGTs can also catalyze the glycosylation reactions of endogenous substrates, plant toxic substances and mycotoxins produced by foreign

organisms including pathogens, for example, the glycosylation of deoxynivalenol (DON) to DON-3-glucoside (D3G) improves the resistance to DON, thus having the function of detoxification and enhancing the resistance of Fusarium head blight in wheat [8,51]. It was confirmed that a glycosyltransferase AtUGT72B1, has high binding activity to pollutants 3,4-dichloroaniline (3,4-DCA) and 2,4,5-trichlorophenol (TCP) in *Arabidopsis* [52]. In addition, the study indicated that AtUGT91C1 plays an important role in the detoxification process of glycosylated herbicides [53]. Thus, UGTs are able to influence the toxicity of herbicides, enhance phytoremediation and degrade the detoxification capacity of organic pollutants. Plant UGTs glycosylate various metabolites and phytohormones, and the active molecules generated are involved in the response of plants to abiotic stress factors such as drought, salt, high temperature and low temperature in the environment [49]. Some studies have reported that plant UGTs improve plant stress resistance by participating in the glycosylation modification reactions of secondary metabolites [10,26].

Conclusion

Plant UGTs play a wide range of glycosylation modifications in secondary metabolic processes, plant hormone regulation and stress response. Recently, with the completion of genome sequencing and assembly of multiple species, genetic and biochemical insights into molecular functions, more UGTs have been explored and identified. However, as a superfamily, the mechanism of action of most members of plant UGTs has not been clearly defined, and there is still a broad exploration space for revealing the functions of UGT family. The functions of UGTs deserve attention and thorough study on enhancing plant resistance against pathogens, bacteriostasis and detoxification, and improving crop yield and quality.

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