# Functional Analysis and the Role of Members of SGT Gene Family of *Withania somnifera*

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**Abstract**

Sterol glycosyltransferases (SGTs) catalyze the attachment of a carbohydrate moiety to an aglycone sterol accepter molecule at different positions. SGTs are key enzymes for the biosynthesis of many precious natural plant products. SGTs of *Withania somnifera* (*Ws*SGTs) help in the glycosylation of withanolides, a pharmaceutically important C-28 phytochemical product and phytosterols, such as sitosterol and stigmasterol. SGTs of *W. somnifera* glycosylate the sterol backbone at C-3, C-17, and C-27 positions. Modified phytosterols and withanolides play an important role in maintaining metabolic plasticity during adaptive response. The expression of SGTs changed during different biotic and abiotic stresses indicating their role in maintaining the cellular disturbances. Overexpression of *WsSGTL1*, a gene member of *SGT* gene family and silencing of *SGT* members through RNAi and artificial miRNA technology, in homologous (*W. somnifera*) and heterologous (*Nicotiana tabacum* and *Arabidopsis thaliana*)

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expression systems defines their role in growth and development of plants. The functional analysis of these genes has also been studied under abiotic (cold, heat, and salt) and biotic (SA, JA, *Alternaria alternata*, and *Spodoptera litura*) stress-providing tolerance to the plants. The chapter is concerned with the importance and application of SGTs in metabolic pathway engineering leading to biosynthesis of important bioactive compounds in *W. somnifera.*

**Keywords**

Glycosyltransferases • *Withania somnifera* • Sterol glycosyltransferases • Biotic and abiotic stresses • *Spodoptera litura* • *Alternaria alternata* • Artificial miRNA • Transgenic plants

## Contents



## 1 Introduction

Plants are the major source of producing a huge diversity of low molecular weight natural products through primary and secondary metabolism. This diversity of compounds is produced by the modification of common backbone structures. Major modifications, such as methylation, acylation, hydroxylation, and glycosylation, play a significant role in maintaining the diversity of compounds in the plant. Glycosylation is one of the most extensive modifications in which monosaccharide molecules attach to the lipids or proteins. Carbohydrates maintain the structural and functional biology of plants, such as in the formation of glycoproteins, proteoglycans, glycolipids, polysaccharides, etc., and have important roles in cell growth, cell-cell interactions, immune defense, etc. [3, 14, 34, 54]. The modifications of protein or lipids by the stepwise assembly of carbohydrate molecules are made by enzymatic process of glycosyltransferases (GTs) which sequentially transfer the monosaccharide carbohydrate molecule from nucleotide donor to the required acceptor, such as lipids, and proteins resulting in the formation of a glycosidic bond [10, 17, 46]. The donor carbohydrates are typically limited to monosaccharides, such as fructose,

galactose, glucose, arabinose, mannose, xylose, etc., linked to a nucleoside mono- or diphosphate, such as cytidine monophosphate (CMP), guanosine diphosphate (GDP), and uridine diphosphate (UDP) [37, 53]. Of these nucleoside sugar donor, more than 60% of all known GTs are reacted by UDP-glycosyltransferases (UGTs) [21]. Consequently, there are many known plant GTs with widely different specificities according to their donor and acceptors. Plant GTs are highly conserved in their sequence and mode of action [5, 15, 35]. They can recognize common features on a range of substrates including secondary metabolites, hormones, or xenobiotics. In *Withania somnifera*, a class of GTs called sterol glycosyltransferases (SGTs) help in the modification of withanolides and other free sterols, such as sitosterol and stigmasterol, for the conversion of its glycosylated forms [48, 51]. In this chapter, we have focused on the importance of SGTs in plants for their tolerance against different stress (biotic and abiotic) conditions.

In CSIR-NBRI, the first biochemical and kinetic properties of SGT were characterized by Madina et al. [30], Madina et al. [29], and Sharma et al. [50]. Chaturvedi et al. [6] described the expression of *sgtl3.1*, *sgtl3.2*, and *sgtl3.3* in biotic (salicylic acid, methyl jasmonate) and abiotic (heat and cold) stresses. Mishra et al. [32] overexpressed the *WsSGTL1* gene in *A. thaliana* and elucidated its role in abiotic stresses (heat, cold, and salt) by the analysis of transgenic lines. Pandey et al. [40] overexpressed *WsSGTL1* gene in *N. tabacum* transgenic lines and in *W. somnifera* for hairy root development and analyzed its role in the production of sterols, glycosylated sterols, and biotic stress (*Spodoptera litura*). Comparative interaction of WsSGTL1 and WsSGTL4 with withanolides and sterols was reported by Pandey et al. [41]. Effect of *WsSGTL1* gene silencing on the growth and glycosylation pattern by RNAi method was reported by Saema et al. [47]. Saema et al. [48] reported that overexpression of *WsSGTL1* in *W. somnifera* helps in growth, enhances glycowithanolides, and provides biotic and abiotic stress tolerance. Further, Singh et al. [51] reported that silencing of some members of *WsSGTs* by aMIR-VIGS system and silencing of genes modulate the withanolide biosynthesis and lines became susceptible to *Alternaria alternata* infection.

## 2 Evolutionary Conserved Nature of *WsSGTs*

Phylogenetic analysis performed in GTs explained the ancient origin during evolution from the time of divergence of prokaryotes and eukaryotes [11, 19]. On the basis of sequence similarity, GTs from prokaryotes to eukaryotes were grouped into four monophyletic superfamilies (named after identified four structural folds) GT-A, GT-B, GT-C, and GT-D. Among them, GT-A and GT-B were evolved as most diverse and ubiquitous group of GTs, as only GT-A includes *E. coli*, *Bacillus subtilis*, *Bos taurus*, *Oryctolagus cuniculus*, *Mus musculus*, *Neisseria meningitidis*, *Homo sapiens*, etc. [28]. According to CAZY online database (http://www.cazy.org/GT1.html), glycosyltransferases (GT) have more than 95 families in which SGTs have been grouped in family 1 because of having a distinct signature motif at the C-terminal, the PSPG domain (Fig. 1) [6, 32].

[FW]-x(2)-[LIVMYA]-[LIMV]-x(4-6)-[LVGAC]-[LVFYA]-
[LIVMF]-[STAGCM]-[HNQ]-[STAGC]-G-x(2)-[STAG]-
x(3)- [STAGL]-[LIVMFA]-x(4)-[PQR]-[LIVMT]-x(3)-[PA]-
x(3)-[PA]- x(3)-[DES]-[QEHN]

**Fig. 1** Highly conserved plant secondary product glycosyltransferases (PSPG) sequences [6]

Full-length characterization of amino acid sequence of *WsSGT* members (*sgtl3.1*-EU342379, *sgtl3.2*-EU342374, and *sgtl3.3*-EU342375) deduced their 45–67% open reading frame (ORF) homonology with known plant's SGTs [7]. Phylogenetic analysis of *WsSGTL1* and *WsSGTL4* proteins reveals the proximity with GTs of *S. lycopersicum* and *M. truncatula*, respectively [29, 41]. GENO3D online server is used for the structured modeling of *Ws*SGTL1 and *Ws*SGTL4 which gives us indications that both proteins belong to GT-B family glycosyltransferase because of having β-sheets in parallel orientation [41]. Studies revealed that almost all members of GT1 family (mostly plant UGTs) have GT-B domain [26, 57].

## 3 Docking of *Ws*SGTL1 and *Ws*SGTL4 with Sterols and Withanolides

Enzymes belonging to the families of glycosyltransferases (GTs) are responsible for the glycosylation of variety of metabolites. The reaction proceeds by the transfer of glycosyl moiety from activated nucleoside diphosphate sugar donor to an acceptor molecule [42]. Two identified SGT enzymes of *W. somnifera*, *Ws*SGTL1 and *Ws*SGTL4, have been compared by Pandey et al. [41] on the basis of their topological character and conserved nature and substrate specificity with different sterols. Differences in size as well as their affinity toward different substrates were observed through sequence alignment and docking experiments, respectively. The obtained results revealed that both WsSGTs show differences in their affinity towards all selected ligands and imply their broad substrate specificity. Among all the tested ligands, brassicasterol and withanolide A showed best interaction to form enzyme substrate complexes with *Ws*SGTL1 and *Ws*SGTL4, respectively [41].

## 4 In Vitro Enzymatic Activity of WsSGTs

The first study of biochemical and kinetic properties of a cytosolic SGT isolated from leaves of *W. somnifera* was performed by Madina et al. [30]. They described that UDP-glucose was sugar donor of that purified enzyme. It had broad glycosylation activity with several sterols and phytosterols with 3β-OH group and low activity with flavonoids and isoflavonoids [29]. The maximum Kcat/Km value of that enzyme was for 24-methylenecholesterol that resembles with sitoindosides VII and VIII of *W. somnifera*. After that Sharma et al. [50] biochemically characterized *WsSGTL1* in *E. coli*. They gave the evidence that the recombinant protein isolated

from *E. coli* showed modification activity with different sterols but not with the salicylic acid [50]. Further, a 27β-hydroxy glucosyltransferase was purified from the cytosolic fraction of *W. somnifera* leaves to study its kinetic and biochemical properties [30]. After characterization, it was proved that purified enzyme showed broad sterol specificity by glycosylating a variety of withanolides/phytosterols with β-OH group at C-17, C-21, and C-27 positions. Singh et al. [51] further reported that silencing of *WsSGTL1*, *WsSGTL2*, and *WsSGTL4* together diminishes their activity in the silenced lines against stigmasterol and solanidine. This study indicated that these genes also participated in the glycosylation of stigmasterol and solanidine.

## 5 Strategies for Functional Analysis of *WsSGTs* Genes

### 5.1 Overexpression in Homologous and Heterologous Expression System

Expression of genes in heterologous organisms has contributed functional importance in animal and plant system. In animal research, *Xenopus* oocytes and cell cultures are major techniques for heterologous gene expression, whereas in plant domain, yeast has become the prevalent heterologous expression system [16, 58]. For the functional analysis of the *SGTL1* gene of *W. somnifera, Arabidopsis thaliana* and *Nicotiana tabacum* were used as heterologous expression systems [32, 40]. Leaves of *N. tabacum* were subjected to *A. tumefaciens*-mediated transformation to develop *WsSGTL1* expressing transgenic lines. Among homozygous T3 plants, three independent highly expressive transgenic lines were selected for further functional analysis. The *WsSGTL1* gene was transformed in *A. thaliana* through *Agrobacterium*-mediated transformation by floral dip method. The phenotypic and physiological parameters like seed weight, germination, root length, shoot weight, relative electrolyte conductivity, MDA content, SOD (and CAT) levels, relative electrolyte leakage, and chlorophyll measurements were compared between transgenic and wild-type *Arabidopsis/Nicotiana* plants. Transgenic *A. thaliana* was observed for tolerance under different abiotic stresses (salt, heat, and cold); however, *N. tabacum* was observed for tolerance to salt stress and biotic (insect) stress to confirm functional importance of *WsSGTL1*. An efficient transformation system of *W. somnifera* for homologus gene expression has also been devloped through transformation of *GUS* reporter gene [38]. Later, Saema et al. [48] introduced *WsSGTL1* gene in homologous system via *Agrobacterium tumefaciens*-mediated transformation [48]. The study proved the use of cotyledonary leaves and hypocotyls explants to get best transformation efficiency. Maximum regeneration and shoot organogenesis of explants were obtained in the presence of 2 mg/l BAP and 0.1 mg/l IAA. Biochemical analysis was done by HPLC-TLC/HPLC and radiolabeled enzyme assay, to confirm the glycosylation achieved by the activity of *Ws*SGTL1. Based on earlier studies, gene-specific primers were used to isolate the full-length open reading frame of *WsSGTL4* (EU342374) from cDNA. By using A4 strain of

*A. rhizogenes*, transgenic hairy root lines with overexpression of *WsSGTL4* gene have been developed [39].

### 5.2 Silencing of *WsSGT* Genes

Gene silencing is a universal word used to explain the regulation of gene expression. For the functional study of *WsSGT* gene members, siRNA and artificial microRNA (amiRNA) technologies have been applied using pFGC1008 and virus-induced gene silencing (VIGS) vectors, respectively [47, 51]. After siRNA-mediated gene silencing of *WsSGTL1* gene, silenced lines were subjected to metabolic profiling of important withanolides. For the functional analysis of a plant gene, virus-induced gene silencing has emerged as powerful tool for the reverse genetics. Silencing of *WsSGTL* members (*WsSGTL1*, *WsSGTL2*, *and WsSGTL4*) with the combination of artificial miRNA and VIGS (aMIR-VIGS) led to the enhanced accumulation of withanolides and phytosterols with decreased content of glycowithanolides in silenced lines. The variations in the concentrations of withanolide in silenced lines resulted in pathogen susceptibility. These results gave indications that a positive feedback regulation of withanolide biosynthesis occurred by silencing of *SGTLs* which resulted in reduced biotic tolerance.

## 6 Biological Roles of *WsSGTs*

### 6.1 Effects of *WsSGTs* on Growth, Development, and Physiology of Plants

Secondary metabolism produces some significant products that assist in the growth and development of plants but are not essential for the plant to survive. Glycosylation is an important phenomenon for the modification of essential secondary plant products during growth and development [2, 9]. This glycosylation can affect the solubility, transport, and biological activity of the hormones. In *W. somnifera*, overexpression of *WsSGTL1* gene positively affects the early and predominant growth [48]. One of the major effects of this overexpression was the increase of 18–38% in stomatal density and increased size of subsidiary cells in progeny of several transgenic lines. This included 42–56% increase in transpiration and stomatal conductance, but it did not affected photosynthetic rate, electron transport, quantum yield, and decreased in water use efficiency. During silencing of *WsSGT* gene members, plants grew with short height and less leaf area, which suggested that *SGT* activity might be affecting the growth hormone signaling pathway in the plants [51]. It has already been reported that the glycosylation of brassinosteroids and strigolactone, a sterol derivative hormone which helps in the growth of axillary bud and plays very important role in the development of plants [6, 22], has been carried out by the members of *SGT*s in plants. Mutation studies on fackel, *SMT1*,

cyclopropylsterol isomerase (*cpi*), *hyd1*, *UGT80B*1, and cotyledon vascular pattern1 (*cvp1*) have revealed roles of sterol modifications in shoot and root patterning, embryo, cell expansion, vein, fertility, polarity, proliferation, gravitropism, hormone signaling, and cellulose level maintenance [4, 12]. An earlier report also revealed cold tolerance, reduced senescence, enhanced growth, and a substantial improvement in protoplasmic drought tolerance, suggesting that SDG8i glucosyltransferase activity might be affecting the strigolactone pathway in the overexpressing lines of *Arabidopsis* [22]. One member of UGTs was reported capable of affecting the biological activity of plant hormones, such as auxins, cytokinins, ABA, SA, jasmonic acid, and brassinosteroids via glycosylation [20, 23, 27, 44]. In heterologous system, expression of *WsSGTL1* reduced plant height and root length and fresh and dry weight of seedling stage of *WsSGTL1-Nt* lines of *Nicotiana tabacum* [40]. Overexpression of *WsSGTL1* gene in *A. thaliana* transgenics showed better seed germination and increased tolerance to salt, heat, and cold stress as compared to wild type [32]. Physiology of plant is dependent on several environmental, biochemical, and molecular changes. Chlorophyll fluorescence imaging (CFI) analysis of *WsSGTL1-Nt* lines revealed reduced fluorescence and absorbance as compared to control plants. Similar to seedlings, 4-month-old *WsSGTL*1-*Nt* plants also showed significantly decreased photochemical efficiency (Fv/Fm) along with lower photosynthetic rate, respiration rate, and stomatal conductance. Similarly, reduced level of chlorophyll-A, chlorophyll-B, total chlorophyll, and carotenoid were found reduced in leaves of 1-month-old and 3-month-old *WsSGTL1-Nt* plants. However, expression of *WsSGTL1* indirectly modulates the growth pattern as well as the physiological properties of *WsSGTL1-Nt* by influencing adaptive machinery of plants similar to reduced growth and photosynthetic rate of plants of severe climatic conditions [40].

## 6.2 Modulates the Glycosylation of Sterols

Cytoplasm and plastids are the compartments for sterol biosynthesis in plant cells by mevalonate pathway of isoprenogenesis through phenyl precursors (Fig. 2) [18]. As an alternative pathway in plants, bacteria, and protozoans, isoprenogenesis is also reported by 1-deoxy-D-xylulose-5-phosphate (DOXP) pathway, which is localized in the plastids [49]. These isoprene units direct the biosynthesis of 2,3-oxidosqualene, which serves as the common precursor of different forms of sterols. Sterol glycosyltransferases (SGTs) in plants catalyze the transfer of glycon moieties to the phytosterols and their related compounds to generate glycoconjugates or steryl glycosides (SGs). SGs are membrane associated sterols and comprised of a sugar moiety attached to C-3 hydroxyl (−OH) group of sterol [7]. For the modification of sterols by SGT enzymes, most preferred position is C-3OH followed by 27β-OH present at the side chain of modified sterols [45, 56]. Enzymatic activity (glycosylating activity) of one member of *WsSGTs*, i.e., *WsSGTL1*, has been reported to have 3β-OH group [29, 31, 50]. Major sterols reported in plant system are sitosterol, campesterol, and stigmasterol having 3β-OH group. These sterols showed activity with

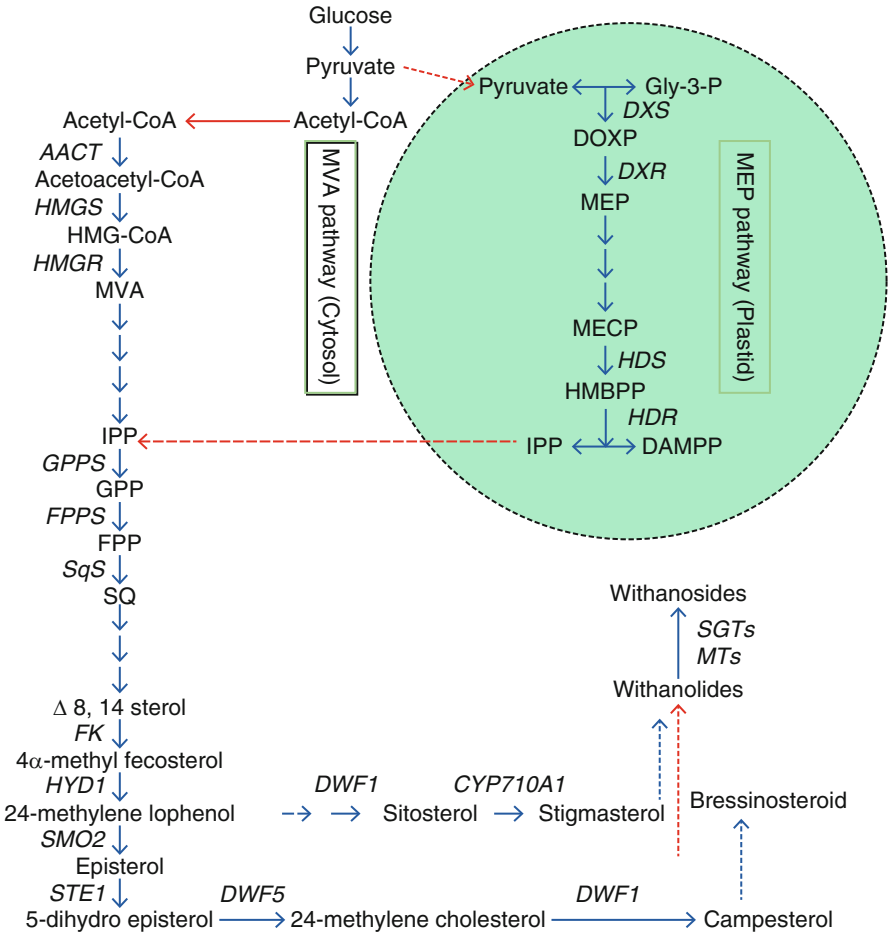


**Fig. 2** Schematic diagram of mevalonate pathway (MVA) of withanoside (glycowithanolides) biosynthesis by the modifications action of SGTs on withanolides

*WsSGTL1*, while another important sterol, i.e., cholesterol, showed no activity with *WsSGTL1* [50]. In *W. somnifera*, SGTs help in the glycosylation of withanolides for the conversion to its glycoconjugates [47, 48, 51]. It was also reported that overexpression of *WsSGTL1* gene modulates the accumulation of glycosylated flavonoids which indicated the role of SGTs in glycosylation of rutin and quercetin [40]. The ratio of glycosylated versus nonglycosylated phytosterols (stigmasterol, sitosterol, and campesterol) also changes after changes in the expression of *WsSGT* in *Withania* or other systems [32, 40, 47, 48, 51]. Till date, hundreds of UDP-glycosyltransferase genes have been cloned and characterized from bacteria, fungus, model and non-model crops, and ornamental and medicinal plants. However, the target of specific *WsSGT* with their specific accepter molecules, withanolides,

flavonoid, or phytosterol in *Withania* is still unknown due to their high sequence and functional similarity.

## 6.3 Role in Abiotic Stress

In plant membrane system, sterols along with lipids have been identified as major components and are necessary for organizing the important events such as protein targeting and signal transduction in plants, fungi, and animals. The expression of *SGTs* maintains the ratio of sterol and sterol glycosides in the plasma membrane by modulating its transcript level under different physiological conditions. Sterol glycosyltransferases (SGTs) are the intermediate enzymes involved in the modification of sterols and play significant role in maintaining the metabolic plasticity during adaptive responses. In *W. somnifera*, *SGTs* are of particular interest for their role in the biosynthesis of pharmacologically active substances [40]. Due to the presence of glycowithanolides in *Withania*, efforts have been made to identify and characterize *SGTs* from this important medicinal plant. Besides their medicinal value, *SGT* gene family members participate significantly different under-changed physiological conditions, growth and development by glycosylation of the growth hormones, and in abiotic and biotic stress conditions [32, 40, 48, 51]. Functional analysis of *WsSGTL1* (a member of *WsSGT* gene family) with its involvement in providing tolerance toward abiotic stresses has been extensively studied by overexpression in *A. thaliana*, *N. tabacum*, and *W. somnifera.* Initially, it was reported that the expression of *WsSGT* members *(WsSGTL1*, *WsSGTL3.1*, *WsSGTL3.2*, and *WsSGTL3.3*) under heat and cold stress indicated their role in abiotic stress tolerance [7]. Further, overexpression of *WsSGTL1* gene into *A. thaliana* showed better germination, salt tolerance, and heat and cold tolerance [32]. The expression level of *WsSGTL1* in the transgenic *A. thaliana* plants was elevated under heat, cold, and salt stress. Comparative study of *UGT80B1* mutant with their restored lines (*p35S*: *TTG15/UGT80B1*) of *A. thaliana* showed that this gene participated in the glycosylation of phytosterols. Due to low level of free and glycosylated sterols in the knockout mutant lines, physiology of plants was highly affected under cold and heat stress [31]. *WsSGTL1* overexpressed *N. tabacum* transgenic lines showed late germination, stunted growth, yellowish green leaves, and enhanced antioxidant system. These changes in the physiological parameters were due to the enhanced glycosylation by *WsSGTL1* gene. Further, overexpression of *WsSGTL1* gene in *W. somnifera* enhanced the ability to recover after cold stress, photosynthesis performance, chlorophyll, anthocyanin content, and quenching regulation of PSI and PSII. These results indicated that the *WsSGTL1* gene participated in the abiotic stress tolerance. Sterol glycosides play important role in membrane fluidity and permeability [58, 59]. Sterol glycosides and acylated sterol glycosides exchange gradually between the monolayer halves of membrane bilayer, in comparison to normal sterols, which serve to regulate sterol content composition and its distribution in the membrane [55, 58]. This modulation of sterols for maintaining the fluidity of biomembrane is the adaptation of plants toward different abiotic stresses [6, 52].

## 6.4 Enhanced Biotic Stress Tolerance

The accumulation of glycosylated sterols in the plant cells gives the tolerance against biotic stress also. There are very few reports available on antibacterial activity, in contrast to antifungal properties of saponins [13]. Silencing of a UDP-Glc-phenylpropanoid glycosyltransferase reduces the accumulation of scopoletin glycoside and weakens virus resistance by enhancing the oxidative stress in the cell [8]. Tomatine is a glycoalkaloid found in the stem and leaves of tomato plants that was reported to have antibacterial and antifungal effects on Gram-positive bacteria [24]. Avenacosides A and B are significant saponins, isolated from oat plants, and have sugar chains at C-3 and C-26 carbons. They lack antimicrobial activity, but by removing the C-26 sugar, it can be converted into biologically active forms. The C-3 position of the sterol moiety is the catalytic target of avenacosides, and these glycoalkaloids were active against the oat root pathogen *Gaeumannomyces graminis* [36]. It was reported that steroidal sapogenins glycosylated by *SAGT4* glycosyltransferase enzyme which catalyzes the 3-O-glycosylation are involved in the biosynthesis of saponin, such as diosgenin, nuatigenin, and tigogenin in *Solanum aculeatissimum* [25]. The involvement of SAGT4 enzyme in response to wounding stress indicates its role in plant defense system. An important potato SGT enzyme SAGT1 was identified by screening a wound-induced cDNA library in yeast suggesting the a possible role of SGT in biotic stress [33]. Brassinosteroids of *A. thaliana* and mycotoxin deoxynivalenol (DON) of *Fusarium* were glycosylated by *UGT73C5* gene which provides protection against the pathogen *Fusarium* by detoxifying DON [43]. The attachment of sugar chain to C-3 of the sterol is usually significant for both antifungal properties, and the permeability of membrane and elimination of these sugar molecules often result in the loss of biological activity of the membrane [1]. Some glycoalkaloid pairs that have common aglycon molecules but differ in the composition of their modified carbohydrate chains show synergism in their membranolytic and antifungal activity [6].

Overexpression of *WsSGTL1* in homologous system provides tolerance toward biotic stress. Transgenic lines prepared by the overexpression of *WsSGTL1* gene in *N. tabacum* and *W. somnifera* increase the insect resistance capacity of the plants, i.e., 100% mortality of *Spodoptera litura*. The larvae consumed a good amount of leaves of WT plants and grew normally, whereas negligible amount of transgenic leaves were fed by larvae. Feeding of *S. litura* larvae on transgenic leaves for 2–4 days resulted in 90–100% mortality. Heterologous system also caused the accumulation of steroidal saponins which increased the insect resistance property of the plants [40, 48]. In addition, in studies using artificial diets, it was proved that increased concentrations of tomatine caused growth retardation and delayed development of beetles feeding on Colorado potato, due to having tetrasaccharide moiety which has membranolytic action [6]. Recently, it was proved that the ratio of glycosylated and free sterols provides tolerance to the plants against the stress of *Alternaria alternata* [51]. SGT enzymes in plants are involved in modulation of sensitivity to stress hormones and changed tolerance to biotic and abiotic stresses [31, 32, 40, 48, 51]. SGTs also glycosylate steroidal hormones such as

brassinosteroids, which has been participating as growth and development regulators in plants. In the field of metabolomics, it can be said that SGTs play significant role in plant metabolism and may offer future tools for crop improvement.

## 7 Conclusions

Sterol glycosyltransferases of *W. somnifera* participated into several physiological, molecular, and biochemical responses. Enzymatic and biochemical analysis of SGTs members indicated their role in modifications of important metabolites which have their own pharmacological value. Functional studies of these family members in homologous and heterologous system indicated their importance in plant system. The members of *SGT* gene family sustain the metabolic plasticity in the cell which maintains the homeostasis of the plants. From the previous research, we can conclude that SGTs maintain several biological processes in the cell, such as increasing the solubilization of compounds, helping in degradation of the xenobiotics, and maintaining the fluidity of membrane by glycosylation of phytosterols. But several important functions still need study in detail, such as how these genes participate in the growth and development and the specific sterol target of specific SGTs.

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