

Plant glycosyltransferases

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Glycosyltransferases are involved in the biosyntheses of cell-wall polysaccharides, the addition of N-linked glycans to glycoproteins, and the attachment of sugar moieties to various small molecules such as hormones and flavonoids. In the past two years, substantial progress has been made in the identification and cloning of genes that encode glycosyltransferases. Moreover, analysis of the recently completed *Arabidopsis* genome sequence indicates the existence of several hundred additional genes encoding putative glycosyltransferases.

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Abbreviations

FT fucosyltransferase
GlcNAc N-acetylglucosamine
Man mannose

Introduction

Glycosyltransferases are enzymes that attach a sugar molecule to a specific acceptor, thereby creating a glycosidic bond. These enzymes are found in most living organisms but are particularly important in plants, which convert the products of photosynthesis into disaccharides, oligosaccharides, and polysaccharides. In addition, glycosyltransferases produce other important molecules including cell-wall polysaccharides, glycoproteins, and many different types of small molecules that have sugars attached to them. Glycosyltransferases have been classified into different families on the basis of the activated molecule that donates the sugar (usually a nucleotide-diphospho-sugar), the type of sugar that they transfer, and whether the enzyme forms an α - or β -glycosidic linkage. Many glycosyltransferases have been identified and studied in plant systems, but knowledge from bacterial, fungal, or animal systems is more advanced and therefore enhances studies in plant systems.

It has been estimated that more than 100 distinct glycosidic linkages are present in the glycoconjugate repertoire of a typical multicellular organism. Because most glycosyltransferases are very specific, it is likely that each different linkage requires the action of a distinct glycosyltransferase, leading to the prediction that multicellular organisms contain hundreds of different glycosyltransferases [1]. The availability of genomic-sequence information has allowed tentative confirmation of this prediction; for example, hundreds of putative glycosyltransferase genes have been

identified in the *Arabidopsis* genome [2••]. Using the sequence-based classification scheme described by Henrissat and colleagues [3••], a summary updated on December 21, 2000, listed 49 families of glycosyltransferases (URL <http://afmb.cnrs-mrs.fr/~pedro/CAZY/gtf.html>). Twenty-five of these families contained representatives from *Arabidopsis*, which had a total of 351 putative glycosyltransferase genes. This accounting is only approximate and the number of *Arabidopsis* genes encoding glycosyltransferases will change as annotation of the genome is refined and as the ability to identify glycosyltransferases on the basis of sequence information is improved.

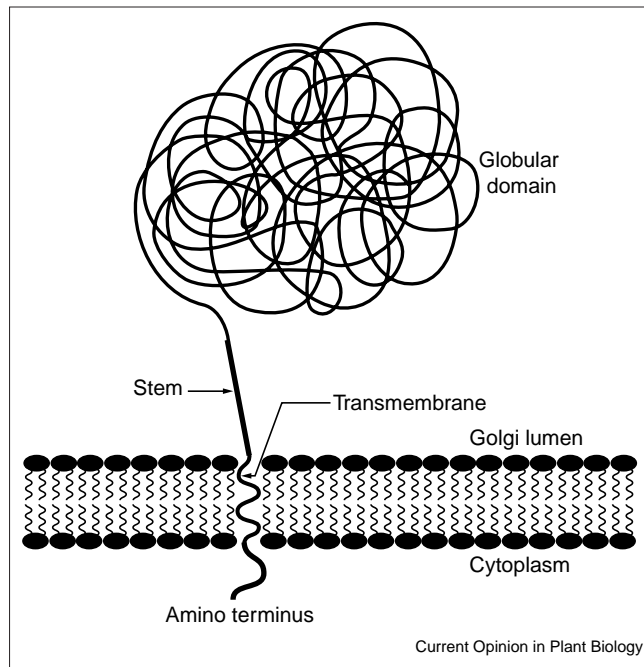
Of these hundreds of putative glycosyltransferase genes, the biochemical activity of the gene product has been confirmed for only a handful. The extreme specificity of many glycosyltransferases increases the difficulty of assessing the biochemical function of the enzymes encoded by these genes. For example, the enzyme that adds fucose to xyloglucan (discussed below) has been utilized to identify a group of nine additional gene products with which it shares extensive sequence similarity, that is, family 37 in Henrissat's scheme [3••]. Preliminary analysis indicates, however, that none of these putative fucosyltransferases use xyloglucan as an acceptor (R Sarria-Milan, A Faik, K Keegstra, N Raikhel, unpublished data). If correct, this raises many important questions about their acceptor specificity as well as their biological functions. Considerable effort will be required to investigate the biochemical and biological function of each of the putative glycosyltransferase genes identified in the *Arabidopsis* genome.

This review highlights some of the advances made over the past two years in our rapidly increasing understanding of plant glycosyltransferases. The glycosyltransferases involved in glycolipid [4,5], starch [6] and sucrose biosynthesis [7] are not considered in this review because of space limitations. Rather, we begin with a consideration of the Golgi enzymes responsible for the synthesis of plant cell-wall polysaccharides, then consider the enzymes in the endoplasmic reticulum and Golgi that are responsible for the modification of plant glycoproteins, before considering the soluble enzymes that add sugars to a wide variety of small molecules.

Glycosyltransferases involved in the biosynthesis of cell-wall polysaccharides

A major feature of plant cells is the presence of a complex wall surrounding virtually every cell. These walls play a crucial role in a multiplicity of processes encompassing growth and development, signal transduction, and cellular responses to environmental factors including pathogens

Figure 1

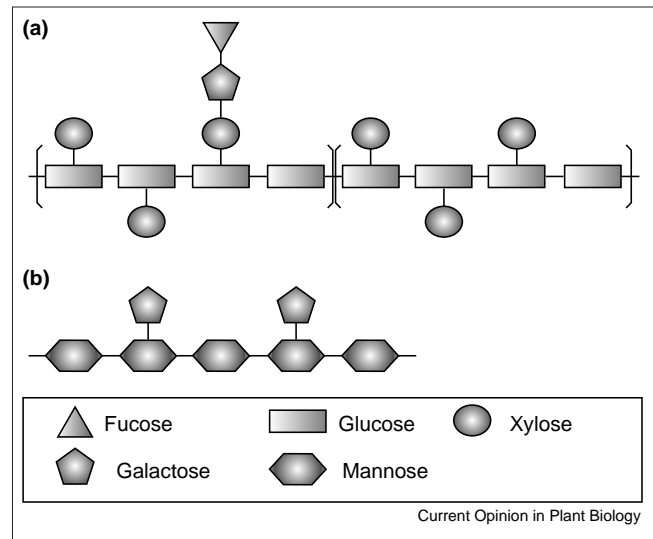


Schematic representation of the topology of most Golgi-localized glycosyltransferases. The amino terminus is located at the cytoplasmic face of the Golgi membrane whereas the globular domain, located near the carboxyl terminus of the protein, is located in the lumen of the Golgi.

and insects. Plant cell walls are typically composed of cellulose microfibrils embedded within a matrix of hemicellulosic and pectic polysaccharides. The biosynthesis of cellulose occurs at the plasma membrane. Some of the genes encoding cellulose-synthase proteins have been identified recently and several reviews cover this topic [8,9]; therefore, we will not deal with it further.

The enzymes involved in glycoprotein and cell-wall-polysaccharide biosynthesis are located within the secretory pathway. Many of these enzymes are type-II membrane proteins possessing a single hydrophobic segment that spans the membrane and functions as a signal-anchor sequence. A short amino-terminal portion faces the cytosol, and the carboxy-terminal catalytic domain is positioned within the lumen of the Golgi apparatus (Figure 1). The biosynthesis of matrix polysaccharides in the Golgi occurs via a process that can be divided into two main stages: the synthesis of the backbone by polysaccharide synthases and the addition of sidechain residues in reactions catalyzed by a variety of glycosyltransferases [10]. Although a number of candidates for genes encoding polysaccharide synthases have been identified [10,11], confirmation of the biochemical function of their gene products is still lacking. We focus here on two recent examples in which the genes encoding two specific glycosyltransferases have been identified and the biochemical functions of their gene products have been confirmed.

Figure 2



Schematic representation of the structure of (a) xyloglucan and (b) galactomannan. Each sugar is shown as a different shape. No attempt is made to depict the position or anomeric configuration of the glycosidic linkages. Parentheses indicate that the enclosed group of sugars are repeated in a regular pattern.

(See also [12] for another recent review that covers this topic.)

Xyloglucan fucosyltransferase

Xyloglucan is the principal hemicellulose of dicotyledonous and non-graminaceous plants. It consists of a β -(1 \rightarrow 4)-linked glucan backbone in which three-fourths of the glucosyl residues are substituted with xylosyl residues in a regular repeating pattern. Some of the xylosyl residues are further decorated with galactosyl and fucosyl residues (Figure 2a).

Recently, a gene encoding a xyloglucan-specific fucosyltransferase has been cloned. Sufficient quantities of this enzyme from pea epicotyls were purified 1400-fold thereby allowing partial amino-acid sequences to be determined. The information deduced from these sequences was used to isolate a fucosyltransferase (FT) cDNA clone (*AtFT1*) from *Arabidopsis* [13**] and from pea (*PsFT1*) [14]. The confirmation of *AtFT1* as a gene encoding a xyloglucan-specific fucosyltransferase was accomplished by analyzing its activity when expressed in a heterologous system, and by immunoprecipitating endogenous activity using antibodies against *Escherichia coli*-expressed *AtFT1* [13**]. Data from the *Arabidopsis* Genome Sequencing Initiative showed that *AtFT1* is located on chromosome 2. A fucose-deficient mutant (*mur2*), originally identified by Reiter *et al.* [15], has recently been shown to be a missense mutation of *AtFT1* (G Vanzin, W-D Reiter, personal communication). Faik *et al.* [14] demonstrated that the purified pea fucosyltransferase is specific for xyloglucan.

Thus, both genetic and biochemical evidence supports the conclusion that the enzymes encoded by these genes are xyloglucan-specific fucosyltransferases.

Examination of the amino-acid sequences of AtFT1 and PsFT1, which are 62.3% identical to each other, explains why it has not been possible to use animal or fungal genes as heterologous probes to isolate genes for plant cell-wall biosynthetic enzymes, despite several attempts by various groups. Neither of these two plant fucosyltransferases shows extensive sequence similarity to fucosyltransferases from other organisms, although short conserved motifs have been identified [14,16,17]. Indeed, in the sequence-based classification scheme of Henrissat and colleagues [3**], these fucosyltransferases are in a separate group (i.e. family 37) from the fucosyltransferases of other organisms. Nine additional *Arabidopsis* genes have, however, been identified that have sequence similarity to *AtFT1*. The extent of similarity to *AtFT1* ranges from 35% to 73.8%, and at least six of these genes are expressed (R Sarria-Millan, K Keegstra, N Raikhel, unpublished data). The biological function of these genes remains unknown: some of them may not even be fucosyltransferases.

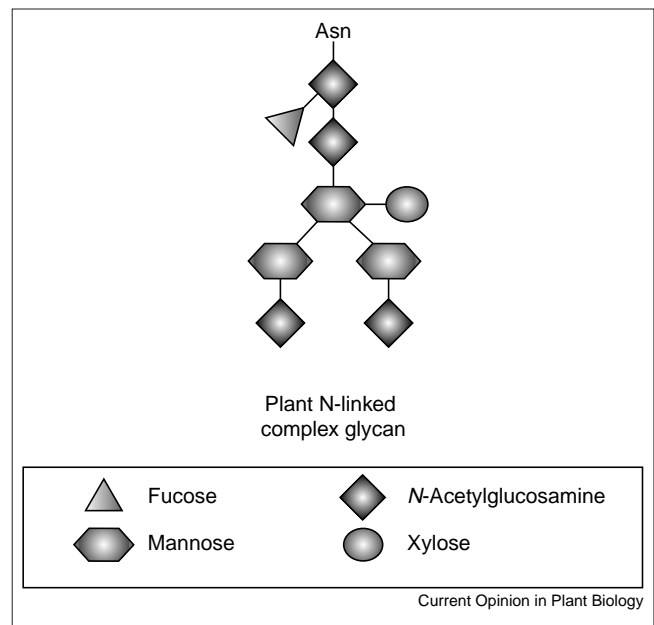
Galactomannan galactosyltransferase

Galactomannans (i.e. α -(1 \rightarrow 6)-galactosyl-substituted (1 \rightarrow 4)- β -D-mannans; Figure 2b) are abundant constituents of legume seed cell walls [18]. Edwards *et al.* [19] developed an assay for a galactomannan galactosyltransferase and showed that high galactomannan galactosyltransferase activity in the endosperm of developing fenugreek (*Trigonella foenum-graecum*) seeds correlated with the presence of a 51 kiloDalton protein [20**]. Sequence from this protein was used to isolate a cDNA clone from the developing endosperm [20**]. The deduced protein encoded by the fenugreek cDNA clone is predicted to have a membrane-spanning region near its amino terminus, which is typical of a type-II membrane protein and characteristic of other glycosyltransferases. The cDNA clone was expressed in yeast (*Pichia pastoris*) to demonstrate that the encoded protein possessed galactomannan galactosyltransferase activity. These results provide convincing evidence that the isolated cDNA clone encoded the fenugreek galactomannan galactosyltransferase. Interestingly, *Arabidopsis* contains eight genes with significant sequence similarity to this fenugreek gene (which is a member of family 34 in Henrissat's classification scheme [3**]).

Biosynthesis of plant glycoproteins

Plants contain several types of glycoproteins, some containing oligosaccharides that are similar to those found in animal and fungal systems and some that are unique to plants. Very little is known about the addition of sugars to arabinogalactan proteins [21] or to hydroxyproline-rich proteins [22], so the glycosyltransferases that are involved in the biosynthesis of these plant-specific glycoproteins are not discussed here. The N-linked glycans that are attached

Figure 3



Schematic representation of the structure of the N-linked oligosaccharides found on many plant glycoproteins. Each sugar is shown as a different shape. No attempt is made to depict the position or anomeric configuration of the glycosidic linkages. Asn, asparagine.

to asparagine residues in many extracellular and membrane proteins are found in plant, animal, and fungal cells. Two types of N-glycans are known: high mannose (Man) glycans (with the composition $\text{Man}_{>5}\text{GlcNAc}_2$ [N-acetylglucosamine]), and complex glycans that have fewer mannose residues and additional residues of other sugars (i.e. fucose, xylose, GlcNAc and galactose). Some complex plant N-glycans are small, containing only two or three mannose residues as well as β -(1 \rightarrow 2)-xylose and α -(1 \rightarrow 3)-fucose (Figure 3) [23], whereas other plant N-linked glycans are larger and have the Lewis antigen structure, a large fucose-containing oligosaccharide [24]. Plant glycoproteins are often extremely immunogenic when used for production of antibodies, and this property may stem from their α -(1 \rightarrow 3)-fucose and β -(1 \rightarrow 2)-xylose residues. It has often been speculated that plant complex glycans are the cause of allergic symptoms in mammals [25].

The basic biosynthetic pathway of high-mannose and complex N-linked glycans is highly conserved among all eukaryotes. The first steps in the pathway are similar or identical in plants and animals [23]. Some genes that encode the glycosyltransferases responsible for these steps have recently been isolated. Using degenerate primers representing highly conserved regions of known N-acetylglucosaminyltransferases from animals, the cDNA coding for transferase I was isolated from a *Nicotiana tabacum* library. The heterologous expression of a predicted catalytic domain from the putative enzyme confirmed the identity of the expected N-acetylglucosaminyltransferase [26*].

Independently from the above-mentioned study, several cDNA clones from potato, tobacco, and *Arabidopsis* encoding N-acetylglucosaminyltransferase I have been isolated and characterized [27•]. The plant N-acetylglucosaminyltransferase possesses 41% identity to known mammalian enzymes with the same specificity.

The differences between high-mannose and complex N-linked glycans arise in later stages of adding terminal sugars. The α -fucosyltransferase catalyzing the transfer of fucose onto the 3-position of the innermost GlcNAc-residue was purified from mung beans. Peptide-sequence information was obtained, and the corresponding cDNA was isolated [28••]. The recombinant fucosyltransferase was expressed in a heterologous system and the specific activity of this enzyme was demonstrated. This plant α -(1 \rightarrow 3)-fucosyltransferase has a relatively low level of identity (28%) with other known enzymes that belong to the same family. Using amino-acid sequences derived from soybean xylosyltransferase [29], the corresponding xylosyltransferase gene was isolated from *Arabidopsis* [30•]. The recombinant protein produced that xylosyltransferase activity *in vivo* [30•]. Using computer searches, non-plant homologs of the *Arabidopsis* β -(1 \rightarrow 2)-xylosyltransferase have not been found to date. All three of the genes encoding glycosyltransferases that mediate decoration of complex glycan in plants are predicted to be type-II membrane proteins and to be localized in the Golgi; their localization and topology have, however, not yet been demonstrated experimentally.

Soluble enzymes that add sugars to small molecules

Although selected genes encoding glycosyltransferases that add sugars to small molecules had been identified before, the pace of their identification has quickened in the past two years and important new advances have been realized. For example, earlier work had identified the gene for adding glucose to the plant growth regulator indoleacetic acid [31]. But in the past two years, several new genes have been identified and the entire gene family has been examined in *Arabidopsis* [32–34,35••]. Similar advances have been made in other areas: genes have been identified for enzymes that add sugars to salicylic acid [36], to flavonoids [37], to sinapic acid and related phenylpropanoids [38], and, finally, to nitriles, thereby creating cyanogenic glucosides [39].

Li *et al.* [35••] used sequences from these and other genes to search the *Arabidopsis* genome for glycosyltransferase genes. As of March 2000, they had found a total of 99 related putative glycosyltransferases (this group is family 1 in Henrissat's classification scheme [3••] and contained 116 putative *Arabidopsis* glycosyltransferase genes on December 21, 2000). This family of plant genes is related to genes found in other organisms. The mammalian enzymes in this family usually transfer glucuronic acid to

small molecules, whereas the plant enzymes normally transfer glucose. However, enzymes that transfer xylose [32] or rhamnose [40] are also present in this family. By constructing a phylogenetic tree that includes not only the *Arabidopsis* genes but also sequences from other species that encode glycosyltransferases with known catalytic activities, the sequences can be arranged into at least twelve groups that appear to be evolutionarily related. As information on the specificity of enzymes in the various groups increases, it should eventually be possible to use such phylogenetic trees to predict not only the evolutionary history but also the substrate specificity of new sequences as they are identified [35••].

Conclusions and future directions

Although significant advances have been made in the identification and characterization of plant glycosyltransferases in the past two years, it seems likely that the pace of this work will accelerate greatly in the years ahead. Future advances will not only build on current knowledge of glycosyltransferases but will also take advantage of important advances unrelated to glycobiology, such as the completion of the *Arabidopsis* genome sequence and the availability of computer programs that can identify sequence similarities among related proteins. For example, the current listing of plant glycosyltransferases does not contain any arabinosyltransferases. Yet knowledge regarding the structure of cell-wall polysaccharides and glycoproteins [21] indicates that plants should have many arabinosyltransferases. Once the first gene encoding a plant arabinosyltransferase is identified, it seems likely that many other candidates will follow quickly from an analysis of the *Arabidopsis* genome sequence.

With these new tools, plant biologists, even now, are inundated with candidate genes that may encode glycosyltransferases. The challenge is to determine the biochemical activity and the biological function of their gene products. Clearly biochemical assays to investigate substrate specificity and expression profiling to examine developmental expression will provide important information with which to address these challenges. Efforts to predict function from sequence similarities, such as those described by Li *et al.* [35••] or Henrissat and Davies [1], combined with enhanced information about the structure–function relationships of glycosyltransferases [41–43] will, however, allow more accurate predictions of the biochemical functions of these newly identified candidates. Thus, the combination of biochemistry, protein-structure studies, genomics and computer analysis of sequences promises to provide rapid advances in understanding plant glycosyltransferases and their important roles in plant biology.

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