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In silico prediction of proteins related to xyloglucan fucosyltransferases in Solanaceae genomes

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Abbreviations: AA, amino acid; AGP, arabinogalactan proteins; FUT, fucosyltransferase; XyG, xyloglucan.

Two independent studies have shown that the cell wall of pollen tubes from tobacco and tomato species contained fucosylated xyloglucan (XyG). These findings are intriguing as many reports have shown that XyG of somatic cells of these species is not fucosylated but instead is arabinosylated. In order to produce fucosylated XyG, plants must express a functional galactoside α -2-fucosyltransferase. Here, using a bioinformatics approach, we show that several candidate genes coding for XyG fucosyltransferases are present in the genome of coffee and several Solanaceae species including tomato, tobacco, potato, eggplant and pepper. BLAST and protein alignments with the 2 well-characterized XyG fucosyltransferases from *Arabidopsis thaliana* and *Pisum sativum* revealed that at least 6 proteins from different Solanaceae species and from coffee displayed the 3 conserved motifs required for XyG fucosyltransferase activity.

Two recent independent studies have shown that the pollen tube cell wall of tobacco (*Nicotiana glauca* and *N. tabacum*) and wild (*Solanum peruvianum* and *S. pimpinellifolium*) and domesticated (*S. lycopersicum*) tomato species contains fucosylated xyloglucan (XyG).^{1,2} We have previously reported in *Arabidopsis thaliana* that the XyG of pollen tubes was also highly fucosylated,³ suggesting an important role of the XyG fucosylation in the pollen tube growth. In all the investigated species, the main fucosylated motif, detected by MALDI-TOF MS after *endo*-glucanase digestion of the XyG, was the mono-acetylated XXFG¹⁻³ according to the nomenclature proposed by Fry et al.⁴ Interestingly, in the cell wall of vegetative organs and/or suspension-cultured cells from plants of the Asterid clade (including the Solanaceae),⁵ XyG lacks fucosyl residues and instead exhibits an arabinoXyG-type, due presumably to an adaptative and/or selective diversification.^{2,6-10} Thus, pollen tubes and vegetative organs from the Solanaceae have structurally divergent XyG. Despite the fact that RNA-Seq analyses of *N. glauca* pollen tubes could not detect any XyG fucosyltransferases,¹ pollen tubes from Solanaceae species must have a specific set of functional XyG fucosyltransferases (FUTs).

In order to find putative XyG FUTs, we used the Basic Local Alignment Search Tool (BLAST) with the sequence of AtFUT1, the well-characterized Arabidopsis XyG galactoside α -2-fucosyltransferase,¹¹ as the reference. AtFUT1 was characterized as a galactoside α -2-fucosyltransferase able to transfer L-fucosyl residues to galactosylated XyG.^{11,12} Two BLAST algorithms were used: the BLAST software of the Sol Genomic Network (<http://solgenomics.net/tools/blast/>) and the BLAST tool of the Uniprot database (<http://www.uniprot.org/blast/>). The BLAST performed in the Sol Genomic Network used the sequence of AtFUT1 against the following databases: the Tomato proteins ITAG (release 2.3), the potato PGSC DM v3.4 protein sequences, the *Nicotiana benthamiana* genome v0.4.4 predicted proteins, the *Capsicum annuum* cv CM334 genome protein sequences, the Eggplant (*Solanum melongena*) Genome protein sequences (release 2.5.1), the *Nicotiana tabacum* TN90 protein sequences and the *Coffea canephora* protein sequences v1.0.

By searching amino acid (AA) sequence similarities with AtFUT1¹¹ the BLAST retrieved several proteins including PsFT1, another characterized XyG FUT from *Pisum sativum*.¹³ PsFT1 showed 59.2% of AA identity with AtFUT1 (Table 1). When the BLAST was performed against the database "tomato

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Table 1. Comparison of the length, identity and similarity of amino acid sequences among 2 galactoside 2- α -L-fucosyltransferases from *Arabidopsis thaliana* (AtFUT1) and *Pisum sativum* (PsFT1) and 15 putative galactoside 2- α -L-fucosyltransferases from *Solanum lycopersicum*, *Solanum tuberosum*, *Solanum melongena*, *Nicotiana benthamiana*, *Nicotiana tabacum* and *Capsicum annuum*. The sequences from all the Solanaceae species were retrieved as a result of sequence similarity search (BLAST) against AtFUT1, using the blast software of the Sol Genomic Network.^{14,15} Identity and similarity were calculated using the BLOSUM 62 matrix. Names, Sequence ID, function or annotation have been retrieved from UniProt or from the Sol Genomic Network.

Organism	Name or sequence ID	Function or annotation	Protein		
			Length	Identity	Code
<i>Arabidopsis thaliana</i>	AtFUT1	Galactoside 2- α -L-fucosyltransferase	558	100%	AtFUT1
<i>Pisum sativum</i>	PsFT1	Galactoside 2- α -L-fucosyltransferase	565	59.2%	PsFT1
<i>Solanum lycopersicum</i>	Solyc07g047920.1	Alpha-1,2-fucosyltransferase	555	57.5%	SIFUTa
<i>Solanum lycopersicum</i>	Solyc06g061210.2	Alpha-1,2-fucosyltransferase	603	55.3%	SIFUTb
<i>Solanum lycopersicum</i>	Solyc03g115830.1	Alpha-1,2-fucosyltransferase	567	53.9%	SIFUTc
<i>Solanum tuberosum</i>	PGSC0003DMG400033900	Alpha-1,2-fucosyltransferase	571	55.8%	StFUTa
<i>Solanum tuberosum</i>	PGSC0003DMG400003781	Alpha-1,2-fucosyltransferase	531	59.2%	StFUTb
<i>Solanum melongena</i>	Sme2.5_14353.1_g00002.1	Unnamed protein product	558	57.9%	SmFUTa
<i>Solanum melongena</i>	Sme2.5_00136.1_g00018.1	Unnamed protein product	501	57.4%	SmFUTb
<i>Nicotiana benthamiana</i>	NbS00022797g0009.1	Putative fucosyltransferase activity	567	51.9%	NbFUTa
<i>Nicotiana benthamiana</i>	NbS00026070g0016.1	Putative fucosyltransferase activity	574	51.9%	NbFUTb
<i>Nicotiana tabacum</i>	mRNA_11650_cds	Fucosyltransferase 7	575	57.6%	NtFUTa
<i>Nicotiana tabacum</i>	mRNA_55231_cds	Fucosyltransferase 7	567	57.1%	NtFUTb
<i>Nicotiana tabacum</i>	mRNA_67630_cds	Fucosyltransferase 7	575	57.8%	NtFUTc
<i>Nicotiana tabacum</i>	mRNA_120465_cds	Fucosyltransferase 7	572	56.7%	NtFUTd
<i>Capsicum annuum</i>	Ca03g29900	Galactoside 2- α -L-fucosyltransferase like	568	54.5%	CaFUTa
<i>Capsicum annuum</i>	Ca06g13300	Galactoside 2- α -L-fucosyltransferase like	551	56.7%	CaFUTb
<i>Coffea canephora</i>	Cc04_g15100	Galactoside 2- α -L-fucosyltransferase	585	53.7%	CcFUTa
<i>Coffea canephora</i>	Cc04_g15110	Galactoside 2- α -L-fucosyltransferase	571	58.6%	CcFUTb
<i>Coffea canephora</i>	Cc00_g15300	Galactoside 2- α -L-fucosyltransferase	463	56.7%	CcFUTc
<i>Coffea canephora</i>	Cc00_g08400	Galactoside 2- α -L-fucosyltransferase	477	54.1%	CcFUTd

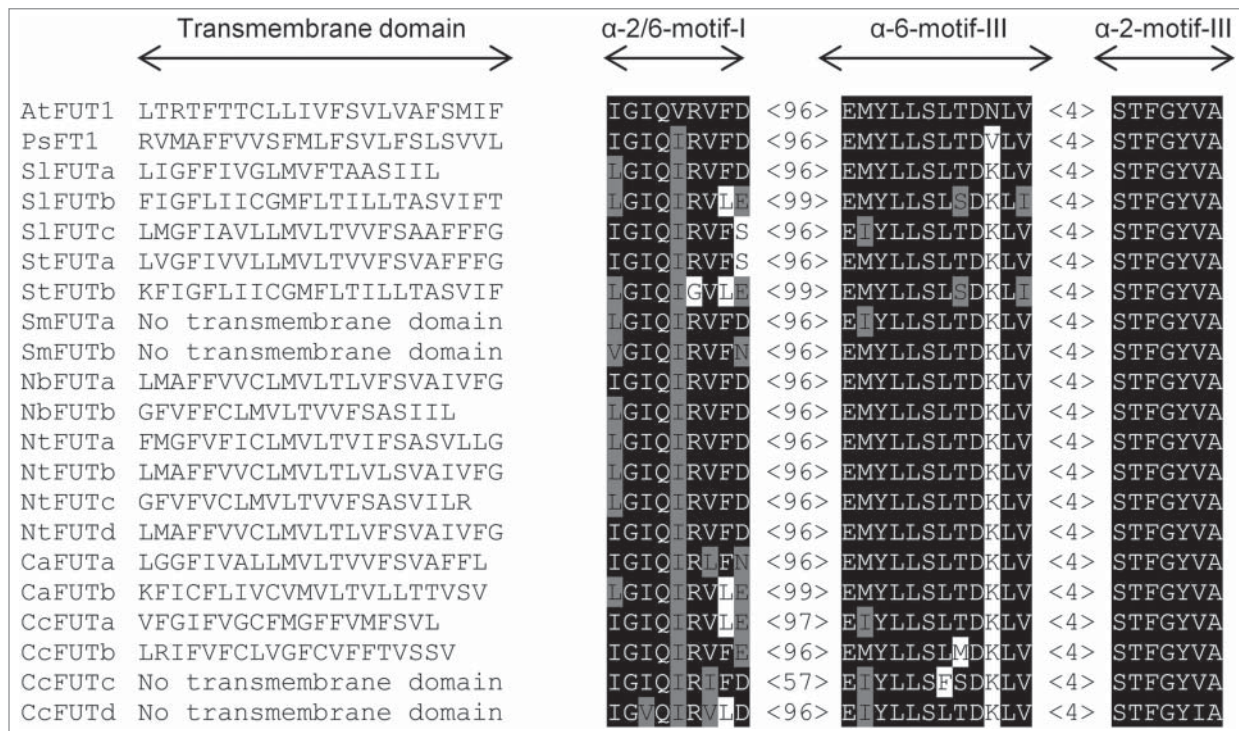


Figure 1. Sequences of the type-II transmembrane domain and the 3 peptide motifs shared by the 2 characterized α -2-fucosyltransferases, AtFUT1 and PsFT1, and the putative α -2-fucosyltransferases from tomato (Sl), potato (St), eggplant (Sm), 2 species of tobacco (Nb and Nt), pepper (Ca) and coffee (Cc). Conserved residues are represented by white letters in black background; highly similar AA are shaded in gray. Numbers inside angle brackets indicate the number of AA between 2 motifs. Proteins are named according to the code used in Table 1.

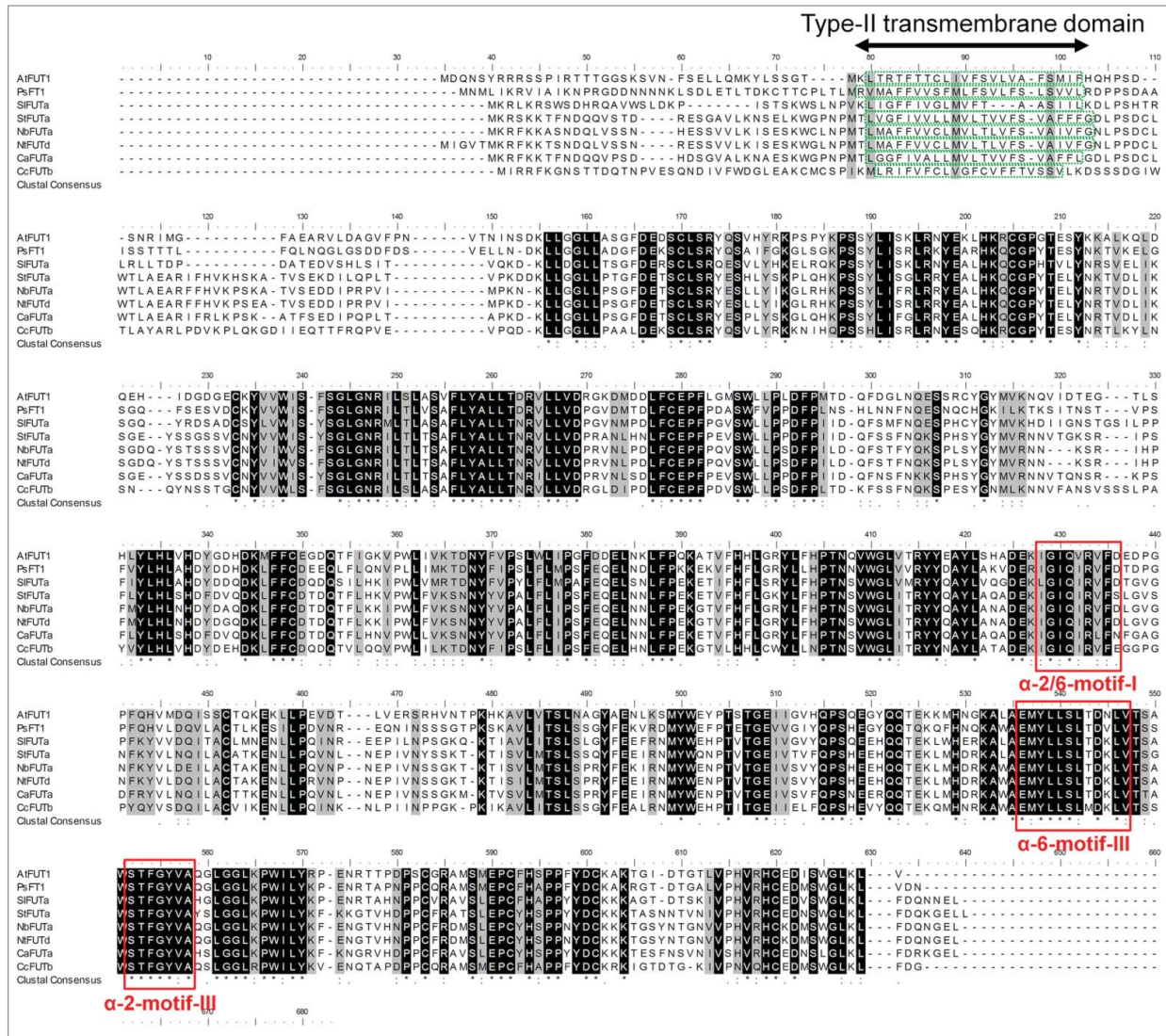


Figure 2. Amino acid (AA) sequence alignments using the ClustalW algorithm. Black and gray shadings represent conserved and highly similar AA, respectively, among the best candidate for putative fucosyltransferases from *S. lycopersicum* (SIFUTa), *S. tuberosum* (StFUTa), *N. benthamiana* (NbfUTa), *N. tabacum* (NfUTd), *C. annuum* (CaFUTa), *C. canephora* (CcFUTb) and the 2 characterized galactoside 2- α -L-fucosyltransferases from *Arabidopsis thaliana* and *Pisum sativum*: AtFUT1 and PsFT1. The type-II transmembrane domains are boxed in green dashed lines. The conserved motifs (α -2/6-motif I, α -6-motif III and α -2-motif III) found in all known α -1,2-fucosyltransferases are boxed in red solid lines. Proteins are named according to the code presented in Table 1.

Proteins ITAG release 2.3," 3 predicted proteins from *S. lycopersicum* coded by the *Soly07g047920.1*, *Soly06g061210.2* and *Soly03g115830.1* genes were tagged as putative fucosyltransferases² (Table 1). These 3 predicted proteins from *S. lycopersicum* displayed 57.5%, 55.3% and 53.9% of AA identity with AtFUT1, respectively. Two putative FUTs were also found in the potato protein sequences, corresponding to the genes *PGSC0003DMG400033900* and *PGSC0003DMG400003781*. These proteins showed 55.8% and 59.2% of AA identity with the sequence of AtFUT1 (Table 1). Two other putative FUTs were found in the genome of *Solanum melongena* with 57.4 and 57.9% of AA identity with AtFUT1. The search in the database of predicted proteins of *N. benthamiana* retrieved 2 sequences

displaying 56.5 and 55.6% of AA identity with AtFUT1 (Table 1). In the *Nicotiana tabacum* genome, 4 genes are predicted to encode FUTs. The proteins showed about 56% of AA identity with the sequence of AtFUT1 (Table 1). In the *Capsicum annuum* genome, 2 putative FUTs coded by *Ca03g29900* and *Ca06g13300* were also found. These putative XyG FUTs from pepper showed 56.7 and 54.5% of AA identity with AtFUT1 (Table 1). Finally, 4 putative XyG FUTs were found in *Coffea canephora* showing between 53.7 and 58.6 % of AA identity with AtFUT1 (Table 1).

AtFUT1 and PsFT1 exhibit a transmembrane domain that is also present in the 15 putative XyG FUTs retrieved in *S. lycopersicum*, *S. tuberosum*, *N. benthamiana*, *N. tabacum*, *C. annuum* and

C. canephora as determined by TMHMM¹⁶ (Fig. 1). This is consistent with FUTs being type-II membrane-bound proteins.^{10,11} However, no transmembrane domain was found neither in the putative XyG FUT from *S. melongena* nor in 2 of the putative XyG FUTs from *C. canephora* (CcFUTc and CcFUTd) (Fig. 1).

It has been shown that all known α -1,2- and α -1,6-FUTs contain 3 conserved motifs, the α -2/6-motif I, the α -2-motif III and the α -6-motif III.^{17,18} Looking in detail at the peptide motifs shared by these putative XyG FUTs (Fig. 1), we can notice that the α -2-motif III is strictly conserved in the 19 predicted proteins and that the α -6-motif III and the α -2-motif III are separated by 4 AA in all the sequences. The α -6-motif III from AtFUT1 and PsFT1 is also conserved with the exception that the asparagine (N) is replaced by a

valine (V) in pea (Fig. 1). In the other putative XyG FUTs from tomato, potato, eggplant, tobacco, pepper and coffee, the α -6-motif III is also very similar to the one found in AtFUT1. Particularly, SIFUTa from tomato, StFUTa from potato, 6 proteins from tobacco, 2 from pepper and SmFUTb from eggplant contained a motif composed of 12 AA. Among them, 11 are identical when compared to the α -6-motif III from Arabidopsis or pea. Only 1 AA differed: the asparagine (N, in Arabidopsis) or the valine (V, in pea) is replaced by a lysine (K) in the Solanaceae sequences (Fig. 1).

The sequences of the α -2/6-motif I from AtFUT1 and PsFT1 is also strictly conserved with the exception that the hydrophobic V in Arabidopsis that is replaced by another hydrophobic AA, isoleucine (I) in pea and the other sequences (Fig. 1). The motif

from pea showed 100% of AA identity with 2 proteins from tobacco (NbFUTa and NtFUTd), 100% of similarity with 1 from tomato (SIFUTa), 4 from tobacco (NbFUTb, NtFUTa, NtFUTb and NtFUTc) and 1 from pepper (CaFUTa) (Fig. 1). In these proteins, with the exception of pepper, the first AA of the motif (I in pea) is replaced by a leucine (L). One sequence from potato (StFUTa) and 1 from tomato (SIFUTc) also contained the motif with a high degree of similarity with PsFT1 with the exception that the last AA of the motif, aspartic acid (D), is replaced by a serine (S) (Fig. 1). These 9 sequences from potato, tobacco, tomato and pepper have also the same gap (96 AA) between the α -2/6-motif I and the α -6-motif III found in AtFUT1 and PsFT1 (Fig. 1). In contrast, the 5 sequences showing the less AA similarity with AtFUT1 and PsFT1 (i.e., SIFUTb, StFUTb, CaFUTb, CcFUTa and CcFUTc) did not contain the 96 AA gap between the α -2/6-motif I and the α -6-motif III (Fig. 1) but displayed a larger gap (97 or 99 AA) or a smaller one of 57 AA (Fig. 1).

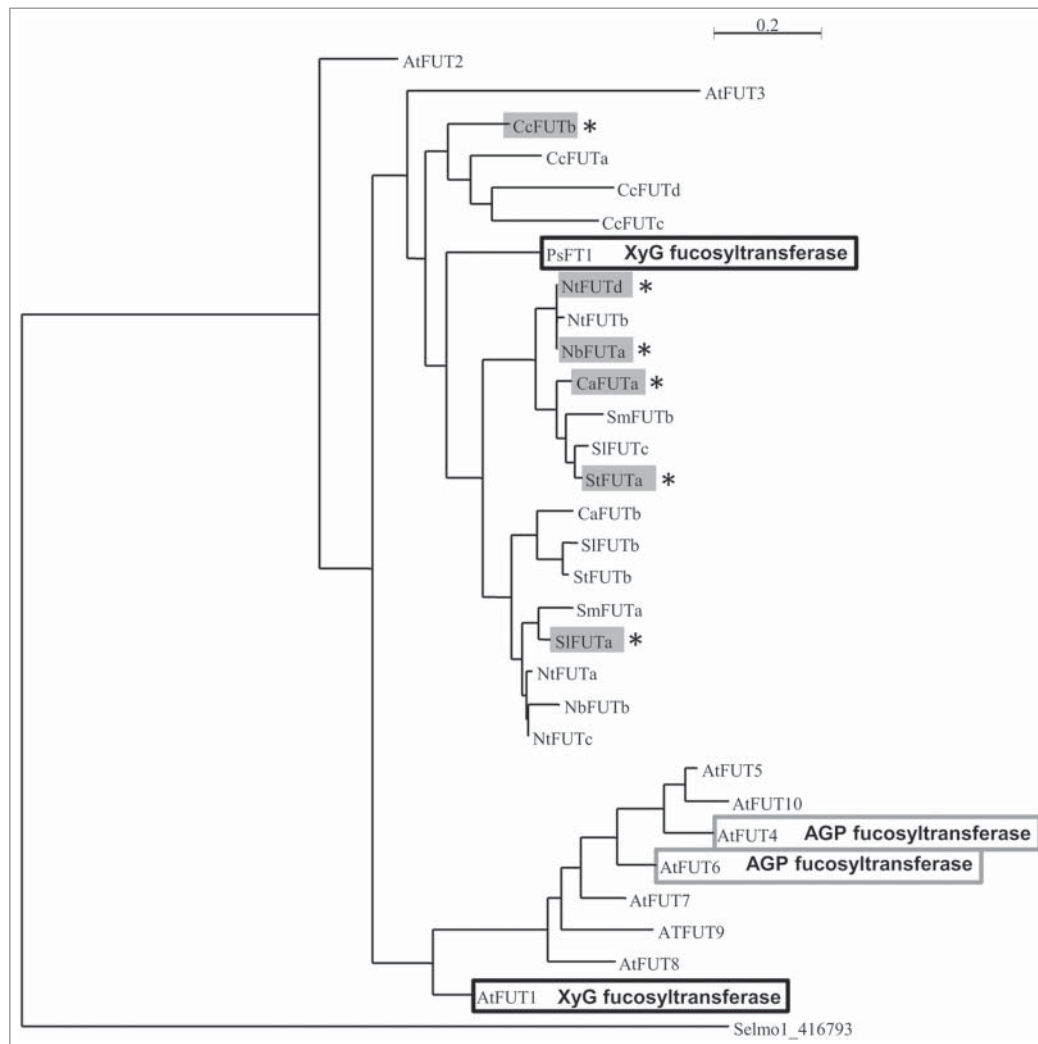


Figure 3. Phylogenetic tree showing the relationships between the AtFUT family and the 19 sequences retrieved in the coffee and the Solanaceae genomes. The tree was generated with MUSCLE for alignment (full processing mode), Gblocks for curation and then built with PhyML (model: WAG; Statistical: alt; Number of categories: 4; Gamma: estimated; invariable sites: estimated) and rendered with Tree dyn. Black boxed sequences correspond to XyG fucosyltransferases, empty gray boxes correspond to AGP fucosyltransferases and painted gray boxes with * correspond to the sequences used for the alignment presented in Figure 2. *A. thaliana* (At), *S. lycopersicum* (Sl), *S. tuberosum* (St), *N. benthamiana* (Nb), *N. tabacum* (Nt), *C. annuum* (Ca), *C. canephora* (Cc), *P. sativum* (Ps), *Selaginella moellendorffii* (Selmo).

In order to visualize the homology of these putative XyG FUTs, we aligned AtFUT1, PsFT1 and the 6 best predicted XyG FUTs from *S. lycopersicum*, *S. tuberosum*, *N. benthamiana*, *N. tabacum* and *C. annuum* and *C. canephora* with the ClustalW algorithm (Fig. 2). The proteins were chosen based on the similarities highlighted in Fig. 1 (presence of the transmembrane domain, identity of the XyG FUT motifs and the gap between the motifs). The alignment revealed that these proteins shared strong similarities (Fig. 2) all along their sequences suggesting that they probably belong to the XyG FUT family.

XyG is not the only polymer containing fucosyl residue linked to galactose in plant cell walls. Among the 10 members of the FUT family in Arabidopsis, 2 of them AtFUT4 and AtFUT6 were characterized as arabinogalactan-protein (AGP) FUT.¹⁹ In order to discriminate if the selected proteins presented in Table 1 may act preferentially on AGPs or on XyG, a phylogenetic analysis was performed. To do so, a predicted XyG FUT from *Selaginella moellendorffii* was used as an outgroup sequence (gene name: GT37A1-1, UniProt D8S0F5). All the sequences from the Table 1 and the 10 sequences of the Arabidopsis FUT family were analyzed using the methods described by Dereeper et al. (2008) (phylogeny.fr).²⁰ Sequences were aligned with MUSCLE (full processing mode), the curation was performed using the Gblocks program to eliminate poorly aligned positions and divergent regions. The phylogeny was performed with PhyML (model: WAG; Statistical: alrt; Number of categories: 4; Gamma: estimated; invariable sites: estimated). Finally the tree rendering was run with Tree dyn and is presented in Fig. 3. Firstly, it appears that the sequences are classified based on the species they belong to except for AtFUT2 and AtFUT3. From the bottom to the top: Arabidopsis, Solanaceae, pea and the coffee FUT families. It appears also that the AtFUT family can be subdivided into

AtFUT1, AtFUT2 and AtFUT3, each in their own group, and AtFUT4 to 10 in a larger group more related to AGP FUTs (Fig. 3). Interestingly, 5 out of the 6 proteins (NtFUTd, NbFUTa, CaFUTa, StFUTa, SIFUTa) aligned with AtFUT1 and PsFT1 (Fig. 2) belong to a large subgroup including PsFT1. The last sequence, from coffee (CcFUTb) belongs to another subgroup (Fig. 3).

The recent discovery of fucosylated XyG in tomato and tobacco pollen tubes implied the presence of functional XyG FUTs. The search of proteins closely related to the well-characterized galactoside α -2-fucosyltransferase, AtFUT1,^{11,21} retrieved, in addition to PsFT1,¹³ 19 predicted proteins in *S. lycopersicum*, *S. melongena*, *S. tuberosum*, *N. benthamiana*, *N. tabacum*, *C. annuum*, and *C. canephora* with the 3 motifs found in all known α -1,2- and α -1,6-fucosyltransferases.^{17,18} Six among these 19 putative XyG FUTs exhibited very strong similarities with AtFUT1 and/or PsFT1 and they are likely to be good candidates to perform the transfer of a fucosyl residue on the galactose of XyG. However, as bioinformatics cannot predict with absolute certainty the donor and the acceptor substrate for these enzymes, experimental evidence is needed to verify in more detail the expression pattern of these genes in pollen grains and pollen tubes and to assess the biochemical functions of these proteins.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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