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**Review**

# Generation of nucleotide sugars for biomass formation in plants

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**Abstract** Nucleotide sugars are activated forms of monosaccharides and serve as glycosyl donors for glycosyltransferases in the synthesis of cell wall polysaccharides. Since they affect the amounts and architecture of cell wall polysaccharides in plants, the levels of nucleotide sugars, as well as the levels of the glycosyltransferases, at least partially, regulate the production of plant cellulosic biomass. Nucleotide sugars are principally generated through *de novo* pathways, in which various UDP- and GDP-sugars are produced through sequential interconversions from starting substrates such as UDP-glucose. The salvage pathway is an alternative route to synthesize nucleotide sugars. In the salvage pathway, free monosaccharides released during the metabolism of polysaccharides and glycoconjugates are first phosphorylated by monosaccharide kinases, and then converted to nucleotide sugars by nucleotide sugar pyrophosphorylases in the presence of the respective nucleotide triphosphates as co-substrates. In this review, we focus on the recent progress in our understanding of the mechanism for the generation of nucleotide sugars through the salvage pathway for free monosaccharides in higher plants.

**Key words:** Cell wall, metabolism, monosaccharide, nucleotide sugar, salvage pathway.

Cellulosic biomass, consisting mostly of cell wall polysaccharides, is the largest biomass on earth. In the synthesis of cell wall polysaccharides, nucleotide sugars, which are activated forms of monosaccharides, serve as glycosyl donors for glycosyltransferases. The availability of nucleotide sugars and the levels of glycosyltransferases affect the amounts and architecture of cell wall polysaccharides in plants. This implies that the levels of nucleotide sugars, at least partially, regulate the production of the cellulosic biomass.

The importance of levels of nucleotide sugars has been demonstrated in Arabidopsis (*Arabidopsis thaliana*) mutants with defects in nucleotide sugar synthesis. Well known is the *mur1* mutant, which has reduced L-fucose (L-Fuc) content in rhamnogalacturonan (RG)-II because of a defect in GDP-mannose (Man) 4,6-dehydratase (EC 4.2.1.47), which catalyzes the first step of conversion of GDP-Man to GDP-L-Fuc in the *de novo* pathway (Bonin et al. 1997). GDP-L-Fuc is indispensable for the boron-mediated dimmer formation of pectic RG-II, and the replacement of L-fucosyl residues by L-galactosyl residues causes dwarf phenotypes (O'Neill et al. 2001). A mutation in the *MUR4* gene encoding a Golgi-localized UDP-xylose (Xyl) 4-epimerase (EC 5.1.3.5) results in a decreased level (50%) of L-arabinose (L-Ara) in cell wall polysaccharides, possibly because of the reduced supply of UDP-L-Ara, the substrate for L-arabinosyltransferases in the Golgi apparatus (Burget and Reiter 1999; Burget et al. 2003). The *reb1-1* mutant, in which a gene for UDP-glucose (Glc) 4-epimerase (EC 5.1.3.2), *AtUGE4*, is mutated, shows altered shape of trichoblasts and growth inhibition of roots, possibly due to lack of galactosyl residues in cell wall polysaccharides such as arabinogalactan-protein and xyloglucan (Andéme-Onzighi et al. 2002; Ngeuma-Ona et al. 2006).

The main routes of nucleotide sugar generation are the *de novo* pathways, in which various UDP- and GDP-sugars are produced through sequential interconversions from starting nucleotides, such as UDP-Glc and GDP-Man (Reiter and Vanzin 2001; Reiter 2008; Seifert 2004; Figure 1). Alternative route in the synthesis of nucleotide sugars is the salvage pathways, where free monosaccharides released during the metabolism of polysaccharides and glycoconjugates are first phosphorylated by the action of monosaccharide kinases,

Abbreviations: L-Ara, L-arabinose; FK, L-fucokinase; FKGP, bifunctional L-fucokinase/GDP-L-fucose pyrophosphorylase; L-Fuc, L-fucose; Gal, galactose; GalA, galacturonic acid; GFPP, GDP-L-fucose pyrophosphorylase; Glc, glucose; GlcA, glucuronic acid; GlcNAc, N-acetylglucosamine; Man, mannose; monosaccharide 1-P, monosaccharide 1-phosphate; L-Rha, L-rhamnose; USP, UDP-sugar pyrophosphorylase; VTC1, GDP-mannose pyrophosphorylase isoform Vitamin C-1; Xyl, xylose. Sugars mentioned in this paper belong to the D-series unless otherwise noted.

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and then converted into nucleotide sugars by nucleotide sugar pyrophosphorylases in the presence of the respective nucleotide triphosphates as co-substrates. Recent studies have suggested that higher plants possess a common salvage pathway for free monosaccharides distinct from the salvage pathways found in mammals and bacteria. Since excellent reviews have provided the details of the enzymes of *de novo* pathway and the related Arabidopsis mutants (Reiter and Vanzin 2001; Seifert 2004; Reiter 2008), we focus here on recent progress in our understanding of the mechanism for the generation of nucleotide sugars through the salvage pathway in higher plants.

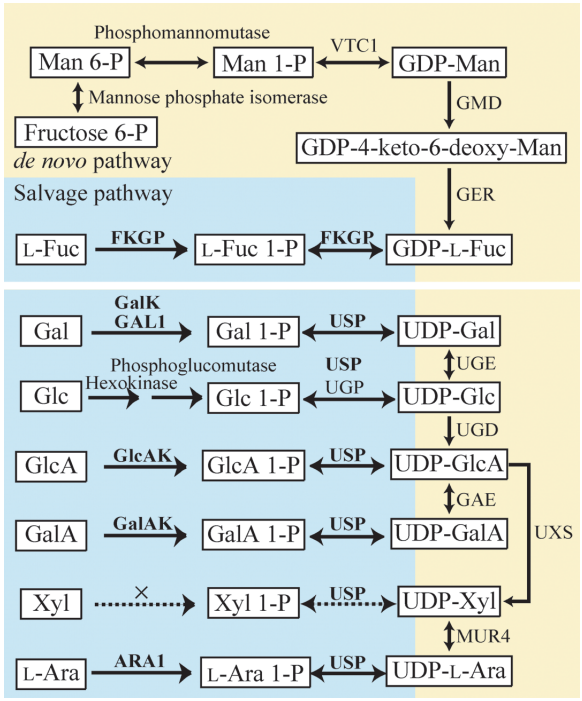


Figure 1. The *de novo* and salvage pathways. The *de novo* and salvage pathways are shown in yellow and blue backgrounds, respectively. The salvage reactions for free L-Ara, GalA, and GlcA have not been reported for vertebrates, fungi, and bacteria. Abbreviations for the enzymes are as follows: GAE, UDP-GlcA 4-epimerase (EC 5.1.3.6); GER, GDP-L-Fuc synthase (GDP-4-keto-6-deoxy-D-mannose-3,5-epimerase/4-reductase, EC 1.1.1.271); GMD, GDP-Man 4,6-dehydratase (EC 4.2.1.47); MUR4, UDP-Xyl 4-epimerase (EC 5.1.3.5); UGD, UDP-Glc dehydrogenase (EC 1.1.1.22); UGE, UDP-Glc 4-epimerase (EC 5.1.3.2); UGP, UDP-Glc pyrophosphorylase (EC 2.7.7.9); UXS, UDP-Xyl synthase (UDP-GlcA decarboxylase, EC 4.1.1.35); VTC1, GDP-mannose pyrophosphorylase (EC 2.7.7.13) isoform Vitamin C-1.

### *Reactions in the salvage pathway*

For the efficient synthesis of cell wall polysaccharides, the generation of nucleotide sugars through the salvage pathway should be advantageous for plants. For example, GDP-L-Fuc is generated from fructose 6-phosphate via four intermediate compounds, Man 6-phosphate, Man 1-phosphate (Man 1-P), GDP-Man, and GDP-4-keto-6-deoxy-Man involving five different enzymes in the *de novo* pathway (Figure 1; Reiter 2008). On the other hand, GDP-L-Fuc can be synthesized from L-Fuc through just two reactions in the salvage pathway (Figure 1; Kotake et al. 2008). The salvage reactions for free monosaccharides are generally composed of two reactions, phosphorylation of the monosaccharides catalyzed by monosaccharide kinases and formation of nucleotide sugars from monosaccharide 1-phosphates (monosaccharide 1-Ps) and the corresponding nucleoside triphosphates by nucleotide sugar pyrophosphorylases.

### *Monosaccharide kinases*

To date, several monosaccharide kinases catalyzing the phosphorylation of monosaccharides have been found in higher plants (Table 1). As had been presumed from the wide occurrence of Gal in nature, galactokinase (EC 2.7.1.6) required for the utilization of free Gal is widely distributed in various organisms including bacteria, fungi, plants, and mammals. The Arabidopsis galactokinase, AtGalK shares significant similarity with galactokinases in mammals (for example, 38% identity to a human enzyme NP_002035). The function

Table 1. Enzymes catalyzing salvage reactions for free monosaccharides in plants

| Enzyme | EC number | Gene lucus[a] | References |
|---|---|---|---|
| Monosaccharide kinases | | | |
| L-Arabinokinase (ARA1) | EC 2.7.1.46 | At4g16130 | Dolezal and Cobbett (1991); Gy et al. (1998) |
| L-Fucokinase (FKGP)[b] | EC 2.7.1.52 | At1g01220 | Kotake et al. (2008) |
| Galactokinase (GalK) | EC 2.7.1.6 | At3g06580 | Kaplan et al. (1997) |
| Galactokinase (GAL1) | EC 2.7.1.6 | At3g42850 | Sherson et al. (1999) |
| Galacturonokinase (GalAK) | EC 2.7.1.44 | At3g10700 | Neufeld et al. (1961); Yang et al. (2009) |
| Glucuronokinase (GlcAK) | EC 2.7.1.43 | At3g01640 | Neufeld et al. (1959); Leibowitz et al. (1977); Gillard and Dickinson (1978); Pieslinger et al. (2009), (2010) |
| Nucleotide-sugar pyrophosphorylases | | | |
| GDP-L-Fuc pyrophosphorylase (FKGP) | EC 2.7.7.30 | At1g01220 | Kotake et al. (2008) |
| UDP-sugar pyrophosphorylase (USP) | EC 2.7.7.64 | At5g52560 | Kotake et al. (2004); Schnurr et al. (2006); Litterer et al. (2006); Kotake et al. (2007) |

[a] Gene locus in Arabidopsis genome is indicated.
[b] FKGP is a bifunctional enzyme having both L-fucokinase and GDP-L-Fuc pyrophosphorylase activities.

of AtGalK has been demonstrated through the complementation of a galactokinase mutant of *Saccharomyces cerevisiae* (Kaplan et al. 1997).

The activity of galacturonokinase (EC 2.7.1.44) was originally reported in mung bean seedlings in 1961 (Neufeld et al. 1961). Recently, Yang et al. (2009) for the first time have identified a gene encoding galacturonokinase, *GalAK*, in Arabidopsis. GalAK has significant sequence similarity with galactokinases, including AtGalK, suggesting that these enzymes evolved from a common ancestor. Yang et al. have also characterized a residue involved in the recognition of the configuration of the OH group at C-4 of galacturonic acid (GalA). The same study shows that mutated recombinant GalAK expressed in *Escherichia coli* has glucuronokinase (EC 2.7.1.43) activity beside its galacturonokinase activity.

By the action of glucuronokinase, free glucuronic acid (GlcA) is phosphorylated to GlcA 1-P, which is then converted to UDP-GlcA in the salvage pathway. Phosphorylation of GlcA also constitutes the *myo*-inositol oxidation (MIO) pathway through which UDP-GlcA is generated from *myo*-inositol via GlcA and GlcA 1-P. Glucuronokinase activity was first found in a soluble fraction of mung bean seedlings in 1959 (Neufeld et al. 1959), and also reported in lily (*Lilium longiflorum*) pollens (Gillard and Dickinson 1978; Leibowitz et al. 1977). Recently, Pieslinger et al. purified the enzyme from lily pollens, and identified *GlcAK* gene encoding glucuronokinase in Arabidopsis (Pieslinger et al. 2009, 2010).

L-Arabinokinase (EC 2.7.1.46) has been identified in a study on the L-Ara-sensitive mutant, *ara1*, which suffers a severe growth defect in the presence of L-Ara. Based on the fact that the growth defect of the *ara1* mutant is not induced by treatment with other sugars, including D-Ara, Gal and Xyl, it has been suggested that the protein encoded by the *ARA1* gene specifically acts on free L-Ara, but not on other sugars (Dolezal and Cobbett 1991; Gy et al. 1998). On the other hand, a homologue related to ARA1, At3g42850, appears to function as a galactokinase on evidence obtained by heterologous expression in the *galk* mutant of *E. coli* (Sherson et al. 1999). Although it is certain that ARA1 and At3g42850 act on L-Ara and Gal, respectively, their substrate specificity toward monosaccharides remains to be determined. Since they have significant sequence similarity, these proteins might have both L-arabinokinase and galactokinase activities.

Phosphorylation of L-Fuc appears to be catalyzed by a bifunctional enzyme. The details of this enzyme will be discussed in a later part of this paper.

### *UDP-sugar pyrophosphorylase*

Monosaccharide 1-Ps formed by monosaccharide kinases are converted to the corresponding nucleotide sugars by the action of nucleotide sugar pyrophosphorylases in the salvage pathway (Figure 1). UDP-sugar pyrophosphorylase (USP, EC 2.7.7.64) is a novel type of nucleotide sugar pyrophosphorylase with broad substrate specificity toward monosaccharide 1-Ps (Kotake et al. 2004; Litterer et al. 2006; Kotake et al. 2007). USP catalyzes the formation of UDP-Glc, UDP-Gal, UDP-GlcA, UDP-GalA, UDP-L-Ara, and UDP-Xyl from respective monosaccharide 1-Ps in the presence of UTP in the salvage pathway (Kotake et al. 2004; Ohashi et al. 2006). One can attribute the activity of UDP-Xyl pyrophosphorylase (EC 2.7.7.11) detected in mung bean seedlings (Ginsburg et al. 1956) to the broad substrate specificity of USP toward monosaccharide 1-Ps. Preceded by the formation of GlcA 1-P by glucuronokinase, the conversion of GlcA 1-P to UDP-GlcA by USP also constitutes a part of the MIO pathway in plants. A loss-of-function mutation in the *AtUSP* gene is not transmitted through the male gametophyte (Kotake et al. 2007; Schnurr et al. 2006). This indicates that the production of UDP-sugars through the salvage pathway or MIO pathway is required for the normal development of pollens (Schnurr et al. 2006). On the other hand, the physiological importance of USP in the vegetative tissues has not yet been studied because no homozygous *usp* mutant could be obtained. A closely related homologue of USP in rice, designated OsUSP (Figure 2), has substrate specificity toward monosaccharide 1-Ps similar to AtUSP, although sugar composition of cell walls differs between rice and Arabidopsis (Kotake and Ando, unpublished results). The fact suggests that USP is conserved and physiologically important in higher plants.

In the purification of glucuronokinase from lily pollens, Pieslinger et al. have established a reliable assay system for glucuronokinase activity. Using recombinant USP expressed in *E. coli*, they converted GlcA 1-P formed by glucuronokinase to UDP-GlcA in the presence of UTP, to be analyzed on high-performance liquid-chromatography (Pieslinger et al. 2009, 2010). This method can be used to assay the activities of other monosaccharide kinases as well.

Except for Glc, which is metabolized in the forms of ADP-Glc, GDP-Glc, and UDP-Glc, each sugar has only one preferred activated form coupling with a particular nucleotide. That is, Gal, GlcA, GalA, L-Ara, and Xyl are metabolized in the form of UDP derivatives, whereas L-Fuc and Man are metabolized as GDP derivatives in higher plants (Figure 1). Consistent with this division in the forms of activated monosaccharides, USP catalyzes the formation of UDP-Gal, UDP-GlcA, UDP-GalA, UDP-L-Ara, and UDP-Xyl from respective monosaccharide 1-Ps and UTP, but fails to convert L-Fuc 1-P and Man 1-P to the respective UDP-sugars (Kotake

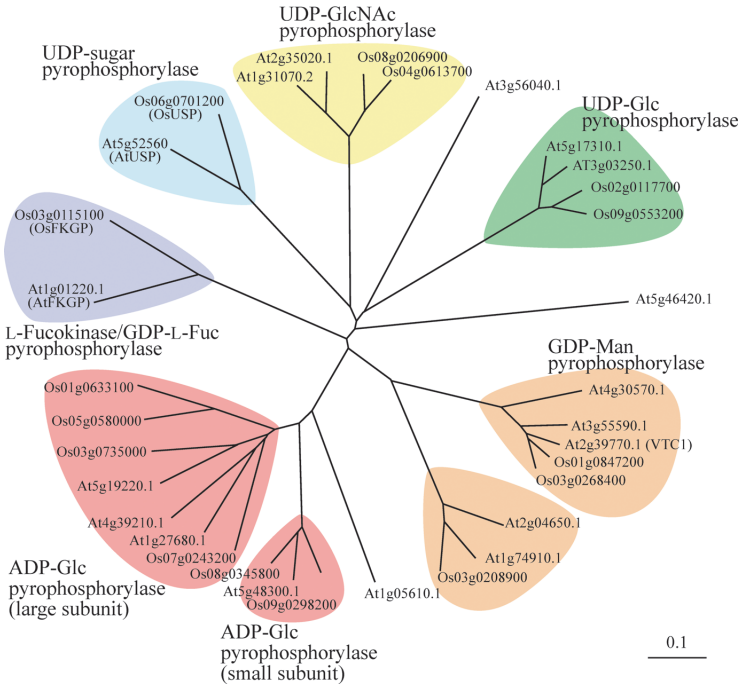


Figure 2. Phylogenetic relationships of nucleotide sugar pyrophosphorylases in Arabidopsis and rice. The phylogenetic analysis was performed using the ClustalW program. The *bar* indicates 0.1 substitutions per site. The initial letter specifies the source of the sequence: At, Arabidopsis; Os, rice.

et al. 2004). It is highly probable that USP recognizes the configurations of OH groups at C-2 and C-3 of sugars. The question of whether this is indeed the case should be clarified through stereochemical analysis of the three dimensional structure of USP.

### *Bifunctional L-fucokinase/GDP-L-Fuc pyrophosphorylase*

As L-Fuc and Man are metabolized as GDP-sugars, the enzymes catalyzing the salvage reactions for L-Fuc and Man are presumed to be distinct from those for Gal, GlcA, GalA, Xyl, and L-Ara. Higher plants have a bifunctional L-fucokinase/GDP-L-Fuc pyrophosphorylase, FKGP, which has low but significant sequence similarity to a bacterial bifunctional enzyme, Fkp (Coyne et al. 2005). FKGP catalyzes the phosphorylation of L-Fuc in the presence of ATP and the conversion of L-Fuc 1-P to GDP-L-Fuc in the presence of GTP, as does Fkp (Figure 1; Kotake et al. 2008). FKGP has a pyrophosphorylase-consensus motif conserved for nucleotide sugar pyrophosphorylases in the N-terminal region and an ATP-binding motif required for the activity of monosaccharide kinases in the C-terminal region. Interestingly, vertebrate L-fucokinases lack a Gly residue highly conserved for plant FKGPs and bacterial Fkps in the pyrophosphorylase-consensus motif, although they share sequence similarity with plant FKGPs (Fig. 3). The vertebrate L-fucokinases probably do not have GDP-L-Fuc pyrophosphorylase activity, because they lack this Gly residue. Indeed, in recombinant Arabidopsis FKGP expressed in *E. coli*, the replacement of the $Gly^{133}$ residue by an Ala residue abolished the GDP-L-Fuc pyrophosphorylase activity (Kotake et al. 2008). Instead, vertebrates perhaps have acquired a GDP-L-Fuc pyrophosphorylase as a separate enzyme to catalyze the conversion of L-Fuc 1-P to GDP-L-Fuc (Figure 3). These facts suggest that plant FKGPs preserved both L-fucokinase and GDP-L-Fuc pyrophosphorylase activities whereas the corresponding vertebrate enzymes lost the GDP-L-Fuc pyrophosphorylase activity in the evolutional process. Because L-Fuc 1-P formed by L-fucokinase activity of FKGP can be utilized as the immediate substrate for GDP-L-Fuc pyrophosphorylase activity without diffusion into the cytoplasm, the bifunctional form likely contributes to the efficient conversion of free L-Fuc to GDP-L-Fuc via L-Fuc 1-P.

### *Priority of metabolism-Perspectives*

The substrate specificity of monosaccharide kinase toward monosaccharides is generally strict, as shown in studies on Arabidopsis ARA1, GalK, GalAK, GlcAK, and FKGP. Given that plants convert all types of free monosaccharides released during the metabolism of cell wall polysaccharides, glycolipids, and glycoconjugates to the corresponding nucleotide sugars, there must be many unidentified monosaccharide kinases including xylokinase (no EC entry), C-1 glucokinase (no EC entry), mannokinase (EC 2.7.1.7), N-acetylhexosamine kinase (EC 2.7.1.162), and L-rhamnokinase (no EC entry) in higher plants. However, not all of these

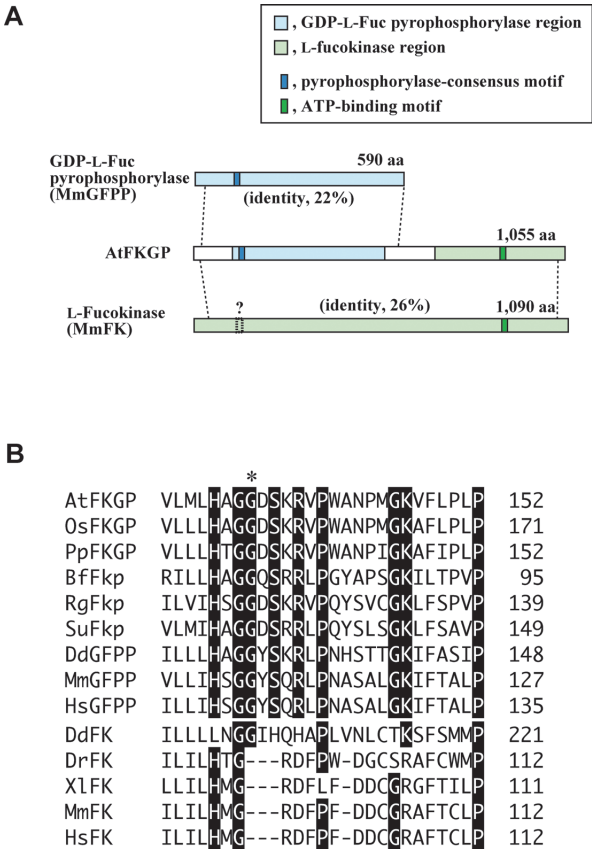


Figure 3. Pyrophosphorylase-consensus motifs of FKGP and vertebrate L-fucokinase. (A) Schematic model of AtFKGP structure. The regions corresponding to L-fucokinase and GDP-L-Fuc pyrophosphorylase are shown in green and blue, respectively. ATP-binding motif conserved for monosaccharide kinase and pyrophosphorylase consensus motif are highlighted with dark green and dark blue boxes, respectively. (B) Sequence alignment of pyrophosphorylase-consensus motifs of plant FKGPs, bacterial Fkps, and vertebrate L-fucokinases and GDP-L-Fuc pyrophosphorylases. The alignment was performed using the ClustalW program. Amino acid residues conserved for FKGPs, Fkps, and vertebrate GDP-L-Fuc pyrophosphorylases are highlighted in black. Gaps(−) were introduced to achieve maximum similarity. The asterisk indicates the $Gly^{133}$ of AtFKGP shown to be required for the GDP-L-Fuc pyrophosphorylase activity. Accession numbers for the clones are as follows: AtFKGP from *Arabidopsis*, At1g01220; BfFkp from *Bacteroides fragilis*, YP_212230; DdFK from *Dictyostelium discoideum*, XP_646182; DdGFPP, XP_638295; DrFK from *Danio rerio*, XP_001344272; HsFK from *Homo sapiens*, NP_659496; HsGFPP, AF017445; MmFK, NP_758487; MmGFPP from *Mus musculus*, AAI10553; OsFKGP from rice, Os03g0115100; PpFKGP from *Physcomitrella patens* subsp. *patens*, XP_001780341; RgFkp from *Ruminococcus gnavus*, ZP_02041638, SuFkp from *Solibacter usitatus*, YP_821860; XlFK from *Xenopus laevis*, NP_001108290.

enzymes do necessarily exist in higher plants, because higher plants probably prefer metabolizing certain types of monosaccharides for their energy, rather than using them to generate nucleotide sugars. For instance, free Glc can be converted to Glc 6-phosphate by the action of hexokinase (EC 2.7.1.1) and metabolized through glycolysis. Free Xyl is perhaps converted to xylulose by the action of xylose isomerase (EC 5.3.1.5), and then to xylulose 5-phosphate by xylulose kinase (EC 2.7.1.17), which is a metabolite in the pentose phosphate pathway. Indeed, neither glucokinase nor xylokinase activity has been reported in plants, although Glc and Xyl are major constituents of cell wall polysaccharides. The question of the priority of metabolism is an important issue that should be resolved, as a better understanding of the mechanism of sugar metabolism may lead to progress in the regulation and efficient production of plant biomass.

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