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Update on Cell Walls

Two General Branching Patterns of Xyloglucan, XXXG and XXGG[1]

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Recent advances in chemical and physical techniques have shed considerable light on the molecular architecture of the primary cell walls of higher plants (for review, see McCann and Roberts, 1991; Carpita and Gibeaut, 1993). According to current models, the primary cell wall is composed of at least two independent polysaccharide networks. The cellulose-xyloglucan network is considered to be an important load-bearing structure of the primary cell wall (Carpita and Gibeaut, 1993). Gaps in the cellulose-xyloglucan network are filled by a network of pectic polysaccharides that may control the porosity of the cell wall (McCann and Roberts, 1991; Carpita and Gibeaut, 1993).

A scale model of the primary cell wall has been constructed on the basis of microscopic studies of onion parenchyma (Fig. 1), and it is likely that the general features of this model are also applicable to parenchyma of other tissues. The primary cell wall (approximately 75 nm thick) is located between the plasma membrane and the middle lamella (approximately 50 nm thick). An important component of the cell wall is cellulose, an unbranched β-D-(1→4)-glucan that associates laterally into microfibrils, each of which is 5 to 12 nm in diameter and of an indeterminate length. The cell wall can accommodate three to four lamellae of cellulose microfibrils. The microfibrils run parallel in each layer and no weaving between layers is observed. Xyloglucans are polysaccharides with a highly branched cellulosic backbone (Hayashi, 1989), which interact intimately with cellulose (McCann and Roberts, 1991; Carpita and Gibeaut, 1993). Chemical extraction of xyloglucans from the cell wall requires conditions such as strongly alkaline solutions, which disrupt the crystalline structure of the cellulose microfibrils. This suggests that a significant part of the xyloglucan is entrapped within cellulose microfibrils (Edelmann and Fry, 1992). The length of individual xyloglucan molecules (30–400 nm) generally exceeds the distance between lamellae many times over, which suggests that these polysaccharides can interconnect several microfibrils (McCann et al., 1992). Typically, xyloglucans appear to be built of blocks of 30-nm repeats, which is approximately the distance between two lamellae. One such repeat corresponds to approximately 60 Glc residues (or 15 oligoglycosyl subunits of the polymer) (for further information, see McCann et al., 1992).

Plant cell walls contain enzymes such as endoglucanases and XET (Fry, 1995; Nishitani, 1995) that can modify the cellulose-xyloglucan network. Endoglucanases can cleave xyloglucan cross-links irreversibly. XETs can cut a xyloglucan chain (the donor substrate) and then reconnect the resulting fragment (containing the nonreducing end of the donor substrate) to another xyloglucan chain (the acceptor substrate). It is expected that these enzymes have a considerable impact on the architecture of the cell wall during cell growth and differentiation. Therefore, considerable attention is being devoted to precisely mapping the mode of action of these enzymes on xyloglucan. Comprehensive analysis of the substrate specificity of these enzymes using all of the different xyloglucans for which structures have been described would be impractical. However, the specificity of these enzymes could be efficiently determined by using a representative set of xyloglucan substrates. In this paper the structural features of xyloglucans are reviewed and representative xyloglucan structures are systematically classified.

Fry et al. (1993) developed a concise nomenclature to unambiguously designate xyloglucan structures. A xyloglucan molecule is named by partitioning the backbone into segments consisting of a single glucosyl residue and its pendant side chains. Each segment is given a specific code letter, depending on the side chain configuration. Thus, the letters "G" and "X" refer to an unbranched β-D-Glc*p* residue and an α-D-Xyl*p*-(1→6)-β-D-Glc*p* segment, respectively. The letter "F" refers to the α-L-Fuc*p*-(1→2)-β-D-Gal*p*-(1→2)-α-D-Xyl*p*-(1→6)-β-D-Glc*p* segment of the fucosylated nonasaccharide (XXFG) commonly found in xyloglucans.

The xyloglucan skeleton is probably assembled by alternate transfer of Glc and Xyl to a nascent polysaccharide having a β-D-Glc*p*-(1→4)- backbone branched with α-D-

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Abbreviation: XET, xyloglucan endotransglycosylase.

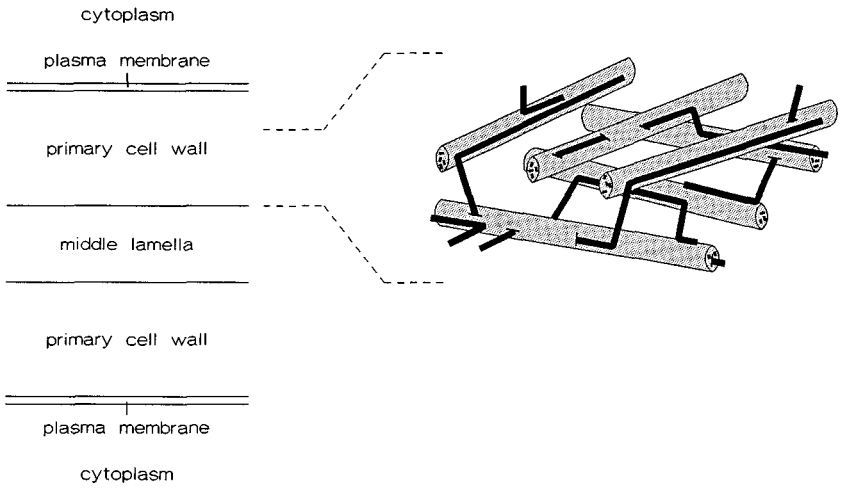

Figure 1. Schematic representation of a part of the cellulose-xyloglucan network in the primary cell wall of plants, adapted from McCann and Roberts (1991). Pectins and proteins, which are also present in the wall, are not shown. Note that the xyloglucan molecules can be incorporated in and bound to the surface of cellulose microfibrils.

Xyl*p*-(1→6)- side chains (Gibeaut and Carpita, 1994). The skeleton is subsequently "decorated" with Gal, Fuc, and/or Ara substituents. The presence of Fuc residues is often regarded as being characteristic of xyloglucans from dicotyledons, because xyloglucans from graminaceous monocotyledons generally lack Fuc residues. However, there may be exceptions to this rule (Hayashi, 1989; McDougall and Fry, 1994), so fucosylation may not be an appropriate criterion for classification. More characteristic, however, are the differences observed in the degree of backbone branching.

Recently, two independent groups suggested that the xyloglucan from solanaceous plants is composed of cellotetraose building blocks (Vincken et al., 1996b; York et al., 1996). Molecular modeling of xyloglucans (Levy et al., 1991) suggests that cellulose binding results from a polymer topology that requires the xyloglucan to be composed of subunits that have an even number of Glc residues in their backbones. These observations have prompted us to compare all known xyloglucan structures with respect to the degree of backbone-branching with Xyl and to comment on several reports in the literature. Most xyloglucans are composed of either XXXG-type or XXGG-type building units (Fig. 2), as discussed below.

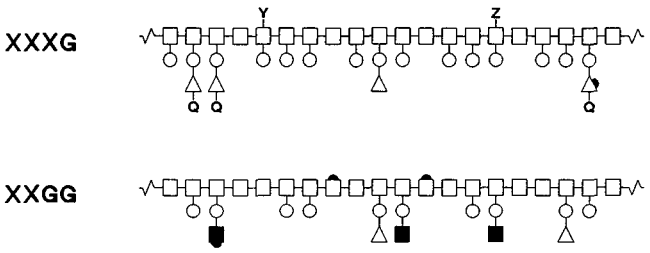

Figure 2. An overview of different branching patterns of xyloglucan. □, β-D-Glc*p*-(1→4)-; ○, α-D-Xyl*p*-(1→6)-; △, β-D-Gal*p*-(1→2)-; and ■, α-L-Ara*f*-(1→2)-. Position Q can be substituted with an α-L-Fuc*p*-(1→2)- residue or an α-L-Gal*p*-(1→2)-. Position Y can be substituted with a β-D-Xyl*p*-(1→2)-, an α-L-Ara*f*-(1→2)-, or an α-L-Ara*f*-(1→3)-β-D-Xyl*p*-(1→2)- side chain. Z can be substituted with a β-D-Xyl*p*-(1→2)- residue. *O*-acetyl groups are indicated by closed half-circles.

POLY-XXXG

This class includes xyloglucans derived from both gymnosperms and angiosperms (York et al., 1990, 1993, 1995; Hisamatsu et al., 1991, 1992; Renard et al., 1992; Hayashi and Takeda, 1994; Ohsumi and Hayashi, 1994; Braccini et al., 1995; Guillén et al., 1995; Vincken, 1996; Vincken et al., 1996a; Wang et al., 1996). We refer to this group as poly-XXXG because three of four Glc residues in the backbone are substituted at *O*-6 with α-D-Xyl*p* residues, resulting in a polymer composed of subunits that have an XXXG core. Some of the Xyl residues are substituted at *O*-2 with β-D-Gal*p* residues. Xyloglucans that are present as storage polysaccharides in seeds such as *Tamarindus indica* (York et al., 1990), cyclamen (Braccini et al., 1995), *Tropaeolum majus* (McDougall and Fry, 1990), and *Detarium senegalense* (Wang et al., 1996) rarely bear any other substituents (no further residues at position Q in Fig. 2). Xyloglucans derived from the cell wall are often fucosylated (i.e. Q is α-L-Fuc*p*-[1→2]-). Oligosaccharides XXFG, XLFG, and XFFG have been characterized in detail (York et al., 1990; Hisamatsu et al., 1991), but the existence of XFLG or XFXG has not yet been demonstrated unambiguously.

In the xyloglucan from a Fuc-deficient *Arabidopsis thaliana* mutant (*mur1*), the α-L-Fuc*p*-(1→2)- residues are replaced by α-L-Gal*p*-(1→2)- residues (Zablackis et al., 1996). The resulting structural element, α-L-Gal*p*-(1→2)-β-D-Gal*p*-(1→2)-α-D-Xyl*p*-(1→6)-β-D-Glc*p*, is defined by the code-letter "J" for jojoba seed, in which this side chain was first detected (Zablackis et al., 1996). The xyloglucan from sycamore seems to be exceptional in that approximately 3% of its backbone residues (i.e. 12% of its cellotetraose-based subunits) bear the unusual side chains (β-D-Xyl*p*-[1→2]-, α-L-Ara*f*-[1→2]-, or α-L-Ara*f*-[1→3]-β-D-Xyl*p*-[1→2]-) at position Y or (β-D-Xyl*p*-[1→2]-) at position Z (Hisamatsu et al., 1992; York et al., 1995). Substitution at these positions renders the adjacent β-Glc*p* residues resistant to endoglucanases. In addition, xyloglucans are often *O*-acetylated. Acetyl groups were detected on the C-2, C-3, or C-6 of Gal residues of the XXFG nonasaccharide derived from sycamore extracellular polysaccharides, as well as from the

cell walls of suspension-cultured sycamore cells (Hayashi, 1989; Kiefer et al., 1989). The Gal residues can contain either one or two acetyl groups. Xyloglucans isolated from various legumes (e.g. pea and common bean) also bear acetyl substituents (W.S. York, M. Pauly, and R. Guillén, unpublished results), but acetyl groups seem to be absent in apple xyloglucan (Renard et al., 1992). The acetyl groups do not provide resistance against the attack of endoglucanases, but their exact function is unknown. So far there has been no clear evidence for the presence of α-L-Ara*f*-(1→2)-α-D-Xyl*p*-(1→6)- side chains in this group, which are commonly found in xyloglucans from solanaceous plants and are discussed below (Hayashi, 1989; York et al., 1996).

POLY-XXGG

Xyloglucans from solanaceous plants have a different branching pattern than the xyloglucans belonging to the poly-XXXG group. These xyloglucans have clusters of two instead of three branched Glc residues, which alternate with a sequence of two "bare" Glc residues (Fig. 2; Vincken et al., 1996b; York et al., 1996). Only about 10% of the tobacco xyloglucan subunits contain a single, isolated branch point (i.e. they are substituted XGGG or GXGG) (York et al., 1996). These structures are consistent with the idea of cellotetraose building blocks. Depending on the origin of the xyloglucan, Xyl residues can be substituted with predominantly α-L-Ara*f*-(1→2)- (tobacco; Hayashi, 1989; York et al., 1996) or α-L-Ara*f*-(1→2)- and β-D-Gal*p*-(1→2)-residues (potato and tomato; Hayashi, 1989; J.-P. Vincken, unpublished results; Vincken et al., 1996b; York et al., 1996). Any combination with Gal and Ara substitution of the Xyl residues seems to occur because SX, XS, and SS (York et al., 1996) and, presumably, LX, XL, LL, and LS (or SL?) (Vincken et al., 1996b) were found in potato xyloglucan. The presence of Fuc, as well as the peculiar substituents at positions Y and Z (Fig. 2), has not (yet) been demonstrated for this group of xyloglucans.

Sims et al. (1996) indicated that α-D-Xyl*p*-(1→2)-α-D-Xyl*p*-(1→6)-β-D-Glc*p* structural elements might be present in XXGG-type xyloglucans secreted by suspension-cultured cells of *Nicotiana plumbaginifolia*. York et al. (1996) demonstrated the presence of a β-L-Ara*f*-(1→3)-α-L-Ara*f*-(1→2)-α-D-Xyl*p*-(1→6)- trisaccharide side chain in tomato xyloglucan and therefore assigned the code letter "T" to this new structural element. In addition, *O*-acetyl groups can be attached to the C-6 position of Glc residues, as in XX(G-ac)G (Sims et al., 1996; York et al., 1996). These *O*-acetyl groups limit the number of possible cleavage sites for endoglucanases during poly-XXGG degradation. *O*-acetyl substituents can also be present on the C-5 of the terminal α-Ara*f* residues of *N. plumbaginolia* xyloglucans (Sims et al., 1996; W.S. York, unpublished results); a small portion of the other bare Glc residue can also carry *O*-acetyl groups (as in [G-ac]XXG; Sims et al., 1996). Typically, xyloglucan is obtained by alkali extraction of cell wall material. During such procedures ester groups are generally removed, and for this reason it is unknown whether *O*-acetylation is a common structural feature in all solanaceous plants.

Because of its lower degree of branching compared with poly-XXXG, the glucan backbone of poly-XXGG can be cleaved by an endoglucanase in a number of different ways, e.g. -XXGG↓*XXGG*↓XXGG-, -XXGG↓*XXG*↓GXXGG-, -XXG↓*GXXG*↓GXXGG-, and -XXG↓*GXXGG*↓XXGG-, yielding different oligosaccharides (Vincken et al., 1996b). It has been shown that two endoglucanases from *Trichoderma viride* differ in their preference for certain linkages: one enzyme releases predominantly XXGG, whereas the other releases XXG, GXXG, and Glc (Vincken et al., 1996b). The diversity of the substitution patterns of poly-XXGG with Ara and Gal residues, as well as the relatively low degree of backbone branching, explain why degradation of this type of xyloglucan by endoglucanase yields such complicated mixtures of oligosaccharides.

OTHER TYPES OF XYLOGLUCANS?

The literature provides a number of reports suggesting that, in addition to poly-XXXG and poly-XXGG, other branching patterns of xyloglucan such as poly-XXG, poly-XXGGG, and poly-XXXX may occur. These patterns will be discussed below.

Poly-XXG

The building units of this type of xyloglucan are composed of two contiguous, branched Glc residues, followed by one unbranched Glc residue. In vitro experiments have suggested that it is possible to synthesize xyloglucan molecules that are composed of XXG building units (Hayashi and Matsuda, 1981; Gordon and Maclachlan, 1989). Degradation of such an "in vitro polysaccharide" by a cellulase preparation did not only yield XXG but also a large amount of monomeric Glc. This suggests that the actual building-unit structure of these polymers corresponds to XXGG, not to XXG. In fact, it may be questioned whether a poly-XXG exists at all. However, xyloglucans often contain isolated XXG subunits. For instance, sycamore (York et al., 1990) and apple (Vincken, 1996; Vincken et al., 1996a) xyloglucans contain small amounts of the XXG-type of oligosaccharides. These may be a result of postdepositional modifications by an α-xylosidase followed by a β-glucosidase (Fry, 1995; Guillén et al., 1995). XET may use such structures as acceptor substrates, producing a xyloglucan molecule with an internal (mid-chain) XXG subunit.

Poly-XXGGG

Xyloglucans derived from immature barley plants (Kato et al., 1981) and rice seedlings (Kato et al., 1982) are insoluble in water, which may be related to their low degree of branching and/or the relatively infrequent substitution of their Xyl residues with Ara or Gal. Although these xyloglucans were hypothesized to be composed of XXGGG-type building units, the presence of XXGGG repeating units was not actually demonstrated. Assuming that these two xyloglucans are composed of cellotetraose-based building blocks, the data presented are consistent with a branching pattern that is predominantly of a XXGG-type,

similar to that of Solanaceae xyloglucans. In addition, approximately 25% of these xyloglucans appear to consist of XGGG- or GXGG-type subunits similar to those present at low abundance in tobacco xyloglucan (see above). The amount of monomeric Glc released upon treatment of these xyloglucans with endoglucanase is too large to be accounted for solely by degradation of the XXGG and XGGG subunits and is consistent with approximately 10% of these xyloglucan preparations being purely cellulosic (i.e. poly-GGGG). However, it is questionable if stretches of GGGG occur as an integral part of the xyloglucan molecule. It is unlikely that GGGG is introduced during biosynthesis of this xyloglucan, because UDP-Xyl is usually required for the enzyme-catalyzed elongation of xyloglucan molecules in vitro (Gordon and Maclachlan, 1989). Addition of UDP-Xyl resulted in elongation and branching of the glucan backbone. Also, incorporation of GGGG into xyloglucan by transglycosylation is difficult to imagine because XET can use neither cellulose as a donor substrate nor cellodextrins as acceptor substrates (Fry, 1995; Nishitani, 1995, and refs. therein). It is possible that a small amount of (1→3)(1→4)-β-glucan was co-purified with the xyloglucan studied by Kato et al. (1981, 1982), and it cannot be ruled out that these two glucans are linked covalently by transglycosylation. It is known that XET does not cleave (1→3)(1→4)-β-glucans (Fry, 1995; Nishitani, 1995), but it has never been investigated whether XET can use these polysaccharides as acceptor substrates. In this respect, it may be important to note that XET and the bacterial (1→3)(1→4)-β-glucanases are assigned to the same protein family (no. 16) (Henrissat, 1994; Nishitani, 1995). Further structural analysis of the xyloglucans produced by the Graminae is required to unambiguously establish whether these polysaccharides are composed of cellotetraose building blocks.

Poly-XXXX

All xyloglucans described thus far contain unbranched Glc residues at regular intervals, making them susceptible to degradation by endoglucanase. An exception to this is a polysaccharide that coats the seeds of *Helipterum eximium* (Mabusela et al., 1990). Every single β-D-Glc*p*-(1→4)- residue is reported to contain two side chains: β-D-Gal*p*-(1→2)-α-D-Xyl*p*-(1→6)- and α-L-Ara*f*-(1→2)-. This polysaccharide was resistant to cleavage by endoglucanase, even after selective removal of the Ara residues with mild acid.

CONCLUSION

We suggest that xyloglucans from different sources show more structural similarity than previously considered. In fact, two general types of xyloglucan, poly-XXXG and poly-XXGG, predominate, although poly-XXXX may also exist. All xyloglucans may thus have a subunit length of four Glc residues but differ in the degree of backbone substitution with Xyl. The data of Hayashi and Matsuda (1981) and Gordon and Maclachlan (1989) suggest that the different forms of xyloglucan may originate from differences in the ability of certain species to mobilize UDP-Xyl. Another interesting observation is that all xyloglucans described to date are composed primarily of subunits that have at least two adjacent, branched Glc residues. Such structures may be required features of the acceptor substrates of some XET isozymes (Lorences and Fry, 1993), but recent data call into question the hypothesis that two adjacent X elements are absolutely required for acceptor substrates of XET. The presence of a GFGGFG structural element in apple fruit xyloglucan suggests that GFG (or GFG on the nonreducing terminus of a larger molecule) is also an acceptor substrate (Vincken, 1996). Fanutti et al. (1996) reported that cleavage of the unbranched Glc residues of xyloglucans by nasturtium XET depends on the presence of specific branched Glc residues in the backbone. For example, for the sequence XXX<u>G</u> ↓ X<u>X</u>XG, the unbranched Glc (underlined G) is cleaved when the branch point indicated by the underlined X is present. The presence or absence of side chains on other Glc residues appears to be less critical. Furthermore, nasturtium XET utilizes acceptor substrates in which the nonreducing-end Glc does not bear a Xyl residue. These results suggest that subunits such as GXGG can be incorporated at a mid-chain position in a xyloglucan molecule, which may explain the relatively large amount of such subunits in tobacco xyloglucan (see above). Therefore, the poly-XXGG xyloglucan from solanaceous plants is a good source of substrates to precisely define the mechanism of action of different XETs (Nishitani, 1995; Vincken, 1996), including the acceptor substrate requirements and the specificity of the site of attack (i.e. XXGG ↓ XXGG- versus -XXG ↓ GXXGG-) of the enzyme.

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