PRIMARY AND SECONDARY PLANT CELL WALLS: A COMPARATIVE OVERVIEW*

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ABSTRACT

Light and transmission electron microscopy are used in studying wall morphology and histochemical methods, including immunocytochemistry, can be used to locate specific compounds in walls. All plant cell walls contain a fibrillar phase of cellulose microfibrils and a matrix phase which contains a high proportion of non-cellulosic polysaccharides that vary in their chemical structures, depending on wall type and plant taxon. The non-cellulosic polysaccharide compositions of three common wall types — lignified secondary walls, non-lignified secondary walls, and non-lignified primary walls — exemplify this. The principles used in constructing the most recent models of non-lignified primary walls can be used in modelling lignified secondary walls.

Keywords: primary cell walls; secondary cell walls; cell-wall models; non-cellulosic polysaccharides; transmission electron microscopy; light microscopy; chemistry; lignified walls; immunocytochemistry; histochemistry

INTRODUCTION

This review provides a brief comparative overview of primary and secondary cell walls of seed plants. A primary wall is defined as a wall that is deposited while the cell is still enlarging, whereas a secondary wall is deposited on the primary wall after cell expansion has stopped, and can be seen in sections as a structurally distinct layer (or layers) that is often very much thicker than the primary wall (Harris 2005a). At maturity, the different cell types can be grouped according to whether they have only a primary wall or both a primary and a secondary wall. For example, parenchyma cells frequently have only a thin primary wall. Cell types with

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secondary walls can be further divided into those with lignified walls, which are the commoner and include sclerenchyma fibres and xylem tracheary elements, and those with non-lignified walls.

Many research groups studying plant cell walls often focus only on either non-lignified primary or lignified secondary walls. For example, groups studying walls in relation to cell enlargement or to food science are often focused only on non-lignified primary walls, whereas groups studying walls in relation to forages for ruminant nutrition or to woods are often focused only on lignified secondary walls. However, I believe there is much to be gained by adopting a broader approach to the study of plant cell walls. In this review, I take an historical approach: I first describe the use of microscopy to study wall morphology, I then describe wall chemistry, focusing particularly on the non-cellulosic polysaccharides, and finally I briefly review wall models.

MICROSCOPY

Plant cell walls were first viewed microscopically in the seventeenth century. Images of cork cell walls were obtained by Robert Hooke, using the compound microscope he built, and were published in his book Micrographia (Hooke 1665). Nehemiah Grew and Marcello Malpighi also carried out some of the earliest anatomical studies on plants and recorded the principal tissues and cell types (Browne 2001). However, it was not until the twentieth century that the terms primary and secondary walls were used as defined above (Kerr & Bailey 1934). Kerr & Bailey (1934) carefully studied the development of tracheids in softwoods and xylem fibres in hardwoods from cambial cells. They related cell expansion to the thickness and morphology of the walls, which they examined using polarised light microscopy. They discovered that the secondary wall layers were not laid down until the cambial cells had stopped enlarging. Moreover, they showed that the secondary walls of softwood tracheids had a three-layered structure and named these layers in the order in which they are laid down: S1, S2, and S3 (Fig. 1) (Bailey & Kerr 1935).

Since the pioneering research of Kerr & Bailey (1934), there have been only a few studies in which cell expansion has been related to the thickness and morphology of the walls. These include studies of the formation of the thick walls of cotton (*Gossypium hirsutum*) fibres (Schubert *et al.* 1973) and of sclerenchyma fibres in the flowering stem of the grass *Lolium temulentum* (Juniper *et al*. 1981). In both studies, it was found that deposition of the "secondary" wall layers began while the cells were still expanding. Other cell types with thick walls that occur outside the secondary xylem may show similar relationships between wall deposition and cell expansion. Simply because a wall is thick does not necessarily mean that it is laid down after expansion has stopped. For example, Majumdar & Preston (1941)

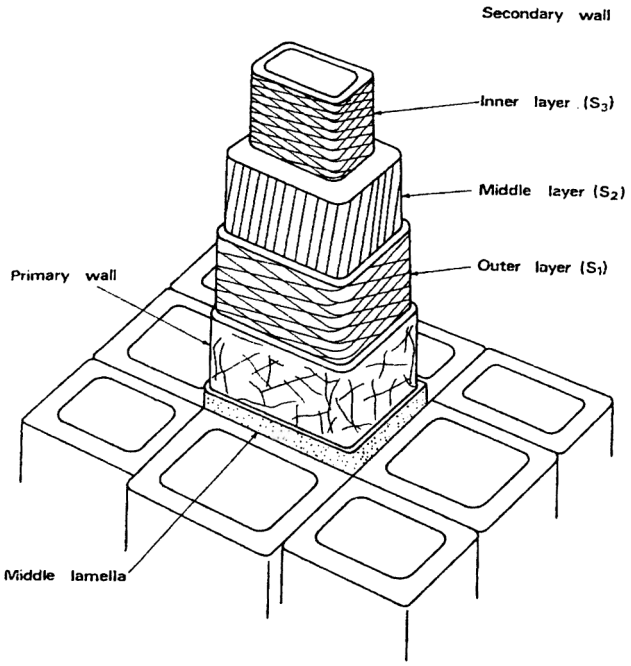

FIG. 1–Simplified diagram of a hardwood xylem fibre or softwood tracheid showing the wall layers and the orientation of the cellulose microfibrils in these layers. [Reproduced from Dinwoodie (1975) with permission].

showed that the thick non-lignified walls of the collenchyma cells in stems of *Heracleum sphondylium* are laid down while the cells are still expanding, and are therefore primary walls.

The invention of the transmission electron microscope enabled cellulose microfibrils to be viewed directly for the first time. The orientation of cellulose microfibrils in the primary walls of growing cells was studied, leading to the development of the multi-net growth hypothesis (Roelofsen & Houwink 1953). The preparative technique of fast-freeze, deep-etch, and rotary shadowing was applied to the study of wall morphology by transmission electron microscopy. In their pioneering study, McCann *et al.* (1990) used this technique to examine the primary walls of onion (*Allium cepa*) and carrot (*Daucus carota*) and discovered cross-links between the cellulose microfibrils. Similar cross-links have since been found using the same technique in the primary walls of a number of species of seed plants (Satiat-Jeunemaitre *et al*. 1992; Fujino & Itoh 1998; Hafrén *et al*. 1999; Fujino *et al*. 2000).

The three secondary-wall layers discovered by Bailey & Kerr (1935) were also observed with transmission electron microscopy, and the orientations of the

cellulose microfibrils in the different wall layers were recorded (Fig. 1) (Frei *et al.* 1957; Wardrop 1965; Dinwoodie 1975; Barnett & Bonham 2004). The preparative technique of fast-freeze, deep-etch, and rotary shadowing was also applied to the study of lignified secondary walls by transmission electron microscopy. Initial studies indicated that the presence of lignin interfered with observations, but when the secondary walls were examined after they were fully formed, and before lignification had occurred, cross-links between cellulose microfibrils were observed (Fujino & Itoh 1998; Hafrén *et al.* 1999; Suzuki & Itoh 2001). Similar cross-links were also observed after lignin had been chemically removed from the walls (Hafrén *et al.* 1999).

More recently the field emission scanning electron microscope and the atomic force microscope have been used to examine cellulose microfibrils in both primary (Sugimoto *et al.* 2000; Davies & Harris 2003; Marga *et al.* 2005) and secondary walls (Abe & Funada 2005; Fahlén & Salmén 2005).

Light and electron microscopy have also been used with specific stains, fluorochromes, and colour reagents to locate particular components in primary and secondary walls. Some of these techniques have been in use for many years. For example, the red colour reaction given by lignin when sections of plant organs are treated with a mixture of phloroglucinol and concentrated hydrochloric acid (the Wiesner reagent) was discovered as long ago as 1878 (Wiesner 1878). Over the last 20 years, immunocytochemistry has increasingly been used to link wall studies using microscopy, to chemical studies. Primary antibodies, both monoclonal and polyclonal, that specifically recognise wall components can be used with secondary antibodies that are labelled either with fluorochromes for detection using fluorescence or confocal laser scanning microscopy, or with colloidal gold particles for detection using transmission electron microscopy (Willats & Knox 2003). Immunocytochemistry is very sensitive and can be used to detect components present in low concentrations. For example, Müsel *et al.* (1997) showed, using immunogold labelling, that low concentrations of lignin occur in the walls of maize (*Zea mays*) coleoptiles. These walls gave no colour reaction with the Wiesner reagent and are usually classified as non-lignified primary walls.

CHEMISTRY

The walls of seed plants are all composed of a fibrillar phase of cellulose microfibrils and a matrix phase containing a high proportion of non-cellulosic polysaccharides that vary in their chemical structures. Structural proteins, glycoproteins, and phenolic components, including lignin, may also be present in the wall matrix (Bacic *et al.* 1988; Harris 2005a). In this review, I focus particularly on the chemical structures of the non-cellulosic polysaccharides in different wall types and plant taxa.

Lignified Secondary Walls

Much of the early chemical work on walls was done using preparations obtained from whole organs, usually of economically important plants. Although few histochemical studies were carried out, many of these studies were done on plant material that was composed almost totally of cells with lignified secondary walls, for example hardwoods, softwoods, and cereal straws. For this reason, the structures of the non-cellulosic polysaccharides in these walls, which vary with plant taxon, were already known by the early 1960s (Timell 1964, 1965; Bacic *et al.* 1988; Harris 2005a).

In the lignified secondary walls of flowering plants (angiosperms), heteroxylans are the predominant non-cellulosic polysaccharides. In hardwoods and other dicotyledons, they are usually 4-*O*-methylglucuronoxylans (Fig. 2), with smaller proportions of glucomannans (Fig. 2). In the large monocotyledon family Poaceae (grasses and cereals), they are mostly glucuronoarabinoxylans (GAXs) (Fig. 2). GAXs have mostly single α-L-arabinosyl and α-D-glucuronosyl (or its 4-*O*-methyl derivative) residues linked at C(O)3 and C(O)2 respectively to the xylose residues of the (1→4)-ß-D-xylan backbone (Carpita 1996; Harris 2000, 2005a). Ferulic acid and small amounts of *p*-coumaric acid are esterified by their carboxyl groups to the C(O)5 hydroxyl of some of the arabinosyl residues (Fig. 2). During the formation of lignin, this ferulic acid becomes incorporated into the lignin, so cross-linking the GAXs and lignin (Ralph *et al.* 2004). In addition, small amounts of (1→3),(1→4)-β-D-glucans, usually considered to be confined to non-lignified primary walls (see below), have been detected by immunogold labelling in the lignified secondary walls of grasses and cereals and some related families (Trethewey & Harris 2002; Trethewey *et al.* 2005). In the walls of other families of commelinid monocotyledons (*see below*), most of the non-cellulosic polysaccharides are probably also GAXs, with similar structures to those in the walls of the Poaceae, whereas in the non-commelinid monocotyledons they are probably usually 4-*O*-methylglucuronoxylans (Harris 2005a).

In contrast to the lignified secondary walls in flowering plants, the non-cellulosic polysaccharides of these walls in coniferous gymnosperms (softwoods) are usually galactoglucomannans (*O*-acetyl-galactoglucomannans) (Fig. 2) and smaller amounts of 4-*O*-methylglucuronoarabinoxylans (Fig. 2). Additionally, the walls of compression wood of coniferous gymnosperms contain two other polysaccharides: a (1→3)-ß-glucan (callose or laricinan) (Fig. 3) and a (1→4)-β-galactan (Fig. 4) (Timell 1986; Bacic *et al.* 1988; Harris 2005b). Using the technique pioneered by Meier (1961) for determining the compositions of wall layers, Côté *et al.* (1968) showed that the (1→4)-β-galactan was located mostly in the S1 layer and outer portion of the S2 layer of the lignified secondary walls of tracheids in the compression wood of balsam fir (*Abies balsamea*).

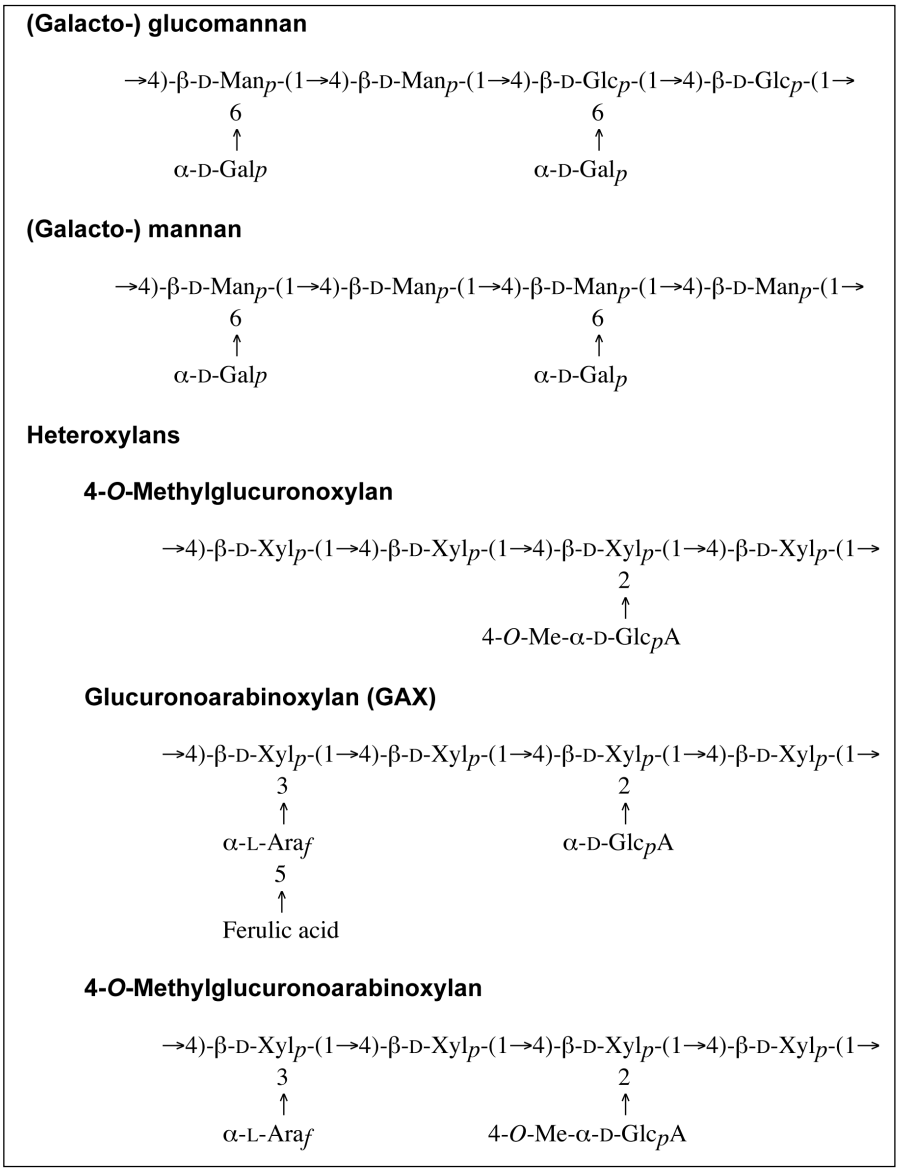

FIG. 2–Structures of heteromannans and heteroxylans that occur in the cell walls of seed plants. For simplicity, sites of possible acetylation are not shown.

Non-lignified Secondary Cell Walls

A number of cell types have thick secondary walls that are not lignified. These include the thick walls of parenchyma cells in the cotyledons and endosperms of many angiosperms seeds, which contain non-cellulosic polysaccharides that function

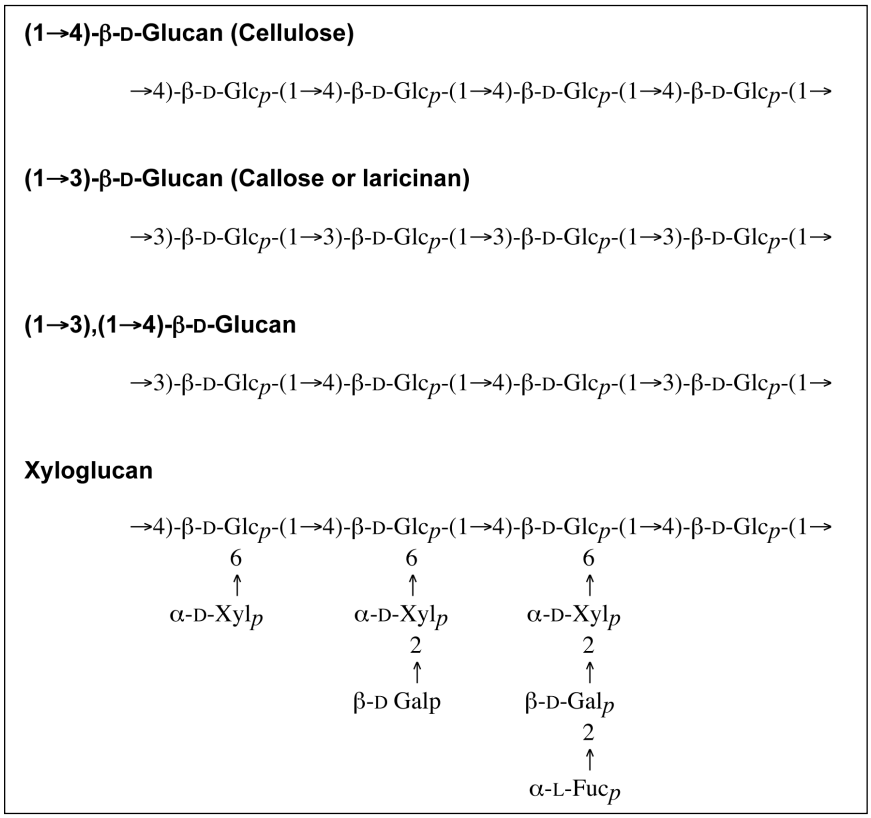

FIG. 3–Structures of glucans that occur in the cell walls of seed plants. Xyloglucans are often acetylated in the cell walls, but for simplicity, the sites of possible acetylation are not shown.

as reserve carbohydrates and are mobilised during germination. As with the non-cellulosic polysaccharides of lignified secondary walls, the structures of these seed-wall polysaccharides were already known in the early 1960s. Excellent historical accounts of these seed polysaccharides have been published by Meier & Reid (1982) and Reid (1985).

In dicotyledon seed walls, one of the following four polysaccharides usually occurs in large proportions: galactomannans, mannans, (1→4)-ß-galactans or xyloglucans (Bacic *et al.* 1988; Buckeridge *et al.* 2000; Harris 2005a) (Fig. 2–4). Galactomannans and mannans occur only in seed walls, but (1→4)-ß-galactans and xyloglucans are also normal components of non-lignified primary walls (*see below*). Galactomannans occur in the endosperm walls of many species of legumes (family Fabaceae), and several other families (Buckeridge *et al*. 2000). Mannans occur in the walls of several species, including *Coffea arabica* (Rubiaceae) (Bacic *et al*. 1988). The (1→4)-ß-galactans occur in the thick walls of some species of *Lupinus* (Fabaceae),

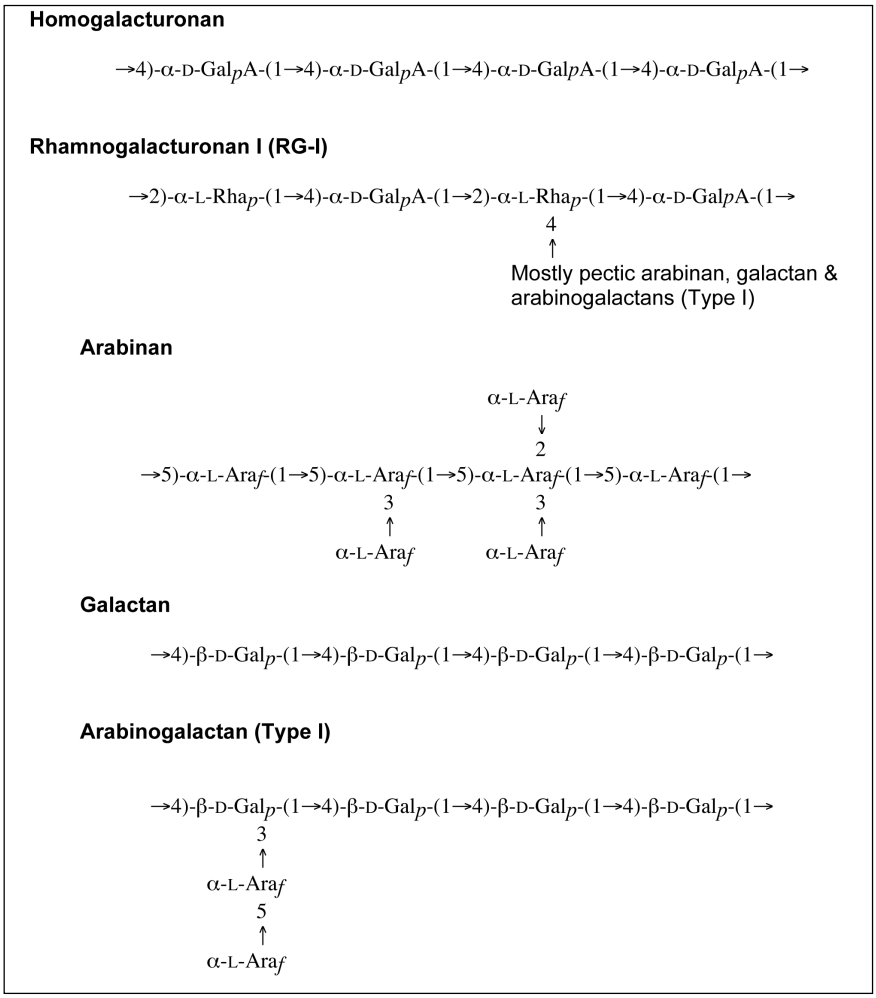

FIG. 4–Structures of pectic polysaccharides that occur in the cell walls of seed plants. The structure of rhamnogalacturonan-II (RG-II) is not illustrated. For simplicity, sites of possible acetylation are not shown.

where they have been detected using immunofluorescence microscopy in conjunction with the monoclonal antibody LM5 (McCartney *et al*. 2000). Xyloglucans occur in the seeds of the Fabaceae (subfamily Caesalpinioidae) and many other families, where they were often referred to as "amyloids" and, in contrast to the xyloglucans in non-lignified primary walls (*see below*), lack fucosyl residues (Kooiman 1960, 1961; Meier & Reid 1982; Reid 1985; Buckeridge *et al*. 2000; Harris 2005a).

In monocotyledons, the thick aleurone walls of Poaceae grains contain GAXs, with only small proportions of glucuronic acid, and (1→3),(1→4)-ß-glucans (Bacic *et al*. 1988; Harris 2005a). In other commelinid monocotyledons (*see below*), the

endosperms of various species of palms (Arecaceae) contain mannans or galactomannans. In the non-commelinid monocotyledons, the endosperms of many species of Asparagales and Liliales contain glucomannans (Meier & Reid 1982; Reid 1985; Bacic *et al*. 1988; Harris 2005a).

Other cell types with non-lignified secondary walls include cotton-seed hairs, which are composed of about 94% cellulose (Fig. 3), and the walls of pollen tubes, which contain a (1→3)-β-glucan (callose) (Fig. 3) (Rae *et al*. 1985; Bacic *et al*. 1988; Stone & Clarke 1992; Ferguson *et al*. 1998).

Non-lignified Primary Walls

In contrast to the non-cellulosic polysaccharide compositions of lignified secondary walls, detailed descriptions of the non-cellulosic polysaccharide compositions of non-lignified primary walls were slower in being obtained. A major reason for this is that it is often difficult to obtain cell-wall preparations uncontaminated by lignified secondary walls (Harris 1983).

Detailed descriptions of the non-cellulosic polysaccharides compositions of the primary walls of dicotyledons started to emerge only in the early 1970s with the work of Albersheim's group using cell-suspension cultures of sycamore (*Acer pseudoplatanus*) that contained no cells with lignified walls. They found that the non-cellulosic polysaccharides of these walls were principally pectic polysaccharides together with smaller proportions of xyloglucans (Talmadge *et al*. 1973; Bauer *et al.* 1973). This was the first time that xyloglucans had been identified as components of primary walls, although structurally similar xyloglucans, but lacking fucosyl residues, were already well known as constituents of non-lignified secondary walls in many seeds (*see above*). The pectic polysaccharides of the primary walls of dicotyledons, including those of sycamore, are highly complex polymers usually composed of three domains: homogalacturonan, rhamnogalacturonan I (RG-I), and small proportions of rhamnogalacturonan-II (RG-II). The homogalacturonan domain is composed of linear chains of galacturonic acid residues that may be methyl-esterified (Fig. 4). RG-1 and RG-II were first characterised in the walls of sycamore suspension-culture cells by Albersheim's group. RG-1 is composed of alternating galacturonic acid and rhamnose residues. Many of the rhamnose residues have oligosaccharide or polysaccharide side chains rich in arabinose and/or galactose that include arabinans, (1→4)-ß-galactans, and Type I arabinogalactans (Fig. 4); however, it is not known if these polysaccharides are always attached to an RG-I backbone (McNeil *et al*. 1980; O'Neill *et al*. 1990; An, O'Neill, Albersheim, & Darvill 1994; An, Zhang, O'Neill, Albersheim, & Darvill 1994; Lerouge *et al*. 1993; Azadi *et al.* 1995). RG-II, which was first described in 1978 (Darvill *et al*. 1978), is a highly complex polymer that contains 12 different glycosyl residues and

more than 20 different glycosyl linkages. Detailed descriptions of the structure of this polysaccharide have been given by Harris (2005a) and O'Neill *et al*. (2004). Small proportions of heteroxylans occur in primary walls of dicotyledons, and the heteroxylan from the walls of sycamore suspension-cultured cells has been characterised as a glucuronoarabinoxylan (GAX) (Darvill *et al*. 1980). This has a similar structure to the GAXs of commelinid monocotyledons, but the side chains are all linked at C(O)2 to the xylose residues of the (1→4)-ß-D-xylan backbone. Small proportions of glucomannans and/or galactoglucomannans (Fig. 2) also occur in primary cell walls of dicotyledons (Bacic *et al*. 1988; Schröder *et al*. 2001).

Research by several groups in the 1970s and early 1980s showed that the non-cellulosic polysaccharide compositions of primary walls of the monocotyledon family Poaceae (grasses and cereals) were quite different from those of dicotyledons. The walls analysed were from cell-suspension cultures (Smith & Stone 1973; Burke *et al*. 1974; Anderson & Stone 1978), coleoptiles (Labavitch & Ray 1978; Wada & Ray 1978; Carpita 1983, 1984a,b), and leaf mesophyll cells (Chesson *et al*. 1985). Instead of containing large proportions of pectic polysaccharides, the walls contain large proportions of glucuronoarabinoxylans (GAXs), variable proportions of (1→3),(1→4)-β-glucans, and small proportions of pectic polysaccharides and xyloglucans (Bacic *et al*. 1988; Carpita 1996; Harris 2000, 2005a). The GAXs (Fig. 2) are more highly substituted than those in lignified secondary walls. (1→3),(1→4)-β-Glucans are linear polysaccharides usually containing 30% (1→3)- and 70% (1→4)-glycosidic linkages (Fig. 3) (Bacic *et al.* 1988; Stone & Clarke 1992; Smith & Harris 1999; Trethewey *et al*. 2005). The structures of the pectic polysaccharides are similar to those in the primary walls of dicotyledons (Carpita 1996; Harris 2000, 2005a), but the structures of the xyloglucans are different: they are less branched, contain no fucose, much less galactose, and less xylose (Vincken *et al*. 1997).

The Poaceae belong to a large group of monocotyledon families, now known as the commelinid monocotyledons, that was initially recognised by the presence of ester-linked ferulic acid in their primary walls and later by the nucleotide sequences of various genes (Harris & Hartley 1980; Harris *et al.* 1997; Harris 2000, 2005a; APG II 2003). With the exception of the palms (Arecaceae) (Carnachan & Harris 2000), the primary walls of this group contain large proportions of GAXs (to which the ferulic acid is esterified) and smaller proportions of pectic polysaccharides and xyloglucans (Smith & Harris 1995, 1999; Harris *et al*. 1997; Harris 2000, 2005a). The presence of (1→3),(1→4)-ß-glucans is restricted to a number of families in the Poales (*sensu lato*) (Smith & Harris 1999; Trethewey *et al*. 2005). The other monocotyledon families, known as the non-commelinid monocotyledons, have primary walls with non-cellulosic polysaccharide compositions similar to those of dicotyledons (Harris *et al*. 1997; Harris 2000, 2005a).

In contrast to the non-cellulosic polysaccharides of lignified secondary walls of coniferous gymnosperms, which were first characterised many years ago, the first detailed study of the non-cellulosic polysaccharides in their primary walls was published in only 1987. This study of the walls of suspension-cultured cells of Douglas fir (*Pseudotsuga menziesii*) (Thomas *et al*. 1987), and subsequent studies of the walls of a number of other species, showed that the non-cellulosic polysaccharide compositions are similar to those of dicotyledon primary walls, although some may contain higher proportions of (galacto-) glucomannans (Harris 2005a).

WALL MODELS

Based on the results of detailed analyses of the walls of cell-suspension cultures of sycamore, Keegstra *et al*. (1973) proposed a model for the non-lignified primary walls of dicotyledons. In this model, the xyloglucans were depicted as being hydrogen-bonded to the cellulose microfibrils, and the pectic polysaccharides as being covalently linked to the xyloglucans and to the glycoprotein extensin. Until very recently, no further evidence was reported for the covalent linkage of pectic polysaccharides to xyloglucans. However, xyloglucans were known to hydrogen bond to cellulose *in vitro*, and Fry (1989) and Hayashi (1989) proposed that xyloglucans could cross-link the cellulose microfibrils in walls. Based on selective extraction of polysaccharides from walls, McCann *et al*. (1990) interpreted the cross-links between cellulose microfibrils they observed by transmission electron microscopy after preparation by fast-freeze, deep etch, and rotary shadowing as being composed of xyloglucans. From these studies, McCann & Roberts (1991) developed a wall model in which a cellulose-xyloglucan network and a pectic polymer network are co-extensive but independent; a third network composed of extensin is also sometimes present. The xyloglucan was assumed to coat completely the surfaces of the cellulose microfibrils. However, two recent findings have resulted in a revision of this model (Fig. 5). First, a study using solid-state ^{13}C NMR spectroscopy showed that in the primary walls of mung beans (*Vigna radiata*) a maximum of only 8% of the surface of the cellulose microfibrils had xyloglucan adsorbed on to it (Bootten *et al*. 2004). Second, despite earlier failures, evidence has been obtained for the widespread occurrence of a covalent linkage between pectic polysaccharides and xyloglucans in primary walls (Popper & Fry 2005; Brett *et al*. 2005; Cumming *et al.* 2005). Both of these findings are incorporated into a revised model (Fig. 5) (Bootten *et al*. 2004).

Models based on similar principles have also been proposed for the primary walls of grasses and cereals (Poaceae) (Carpita 1996; Carpita *et al.* 2001; Harris 2005b). In these walls, the cross-links visible by transmission electron microscopy are considered to be GAXs with backbones carrying few substituents. GAXs with

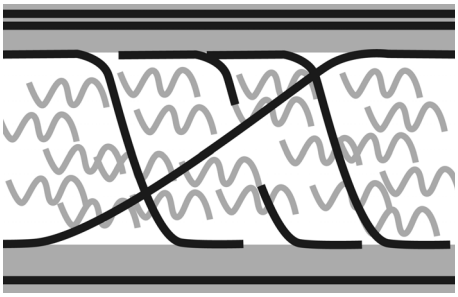

FIG. 5–Model of non-lignified primary walls of dicotyledons as modified by Bootten *et al*. (2004). Xyloglucans (solid black lines) are hydrogen bonded on to only a small proportion of the surface area of adjacent cellulose microfibrils (grey). Some of the xyloglucans cross-link the cellulose microfibrils, others cross-link cellulose microfibrils and pectic polysaccharides (wavy lines).

similar structures, together with (1→3),(1→4)-ß-glucans, have been envisaged as coating the cellulose microfibrils. However, if the results obtained from the walls of mung beans (Bootten *et al*. 2004) apply more widely, only a small proportion of the microfibril surfaces may have non-cellulosic polysaccharides adsorbed to them. GAXs with highly substituted backbones and small proportions of pectic polysaccharides are thought to form the second network.

Models of lignified secondary walls, such as that of Kerr & Goring (1975), often show cellulose microfibrils separated by a matrix containing lignin and non-cellulosic polysaccharides, but no cross-links between the microfibrils. However, as indicated above, cross-links have been observed by transmission electron microscopy in such walls. Thus, it can be argued that similar principles to those used in modelling primary walls can be applied to modelling lignified secondary walls (Harris 2005b). The presence of cross-links in secondary walls suggests that these walls contain a network equivalent to the cellulose-xyloglucan or cellulose-GAX networks described in primary walls. In secondary walls, the compositions of the cross-links are unknown. However, they are probably composed of the following non-cellulosic polysaccharides: in hardwoods and other dicotyledons, 4-*O*-methylglucuronoxylans and/or glucomannans; in grasses and cereals (Poaceae), GAXs; and in softwoods, (galacto-)glucomannans and/or 4-*O*-methyl-glucuronoarabinoxylans. It is likely that, except for the glucomannans, populations of these polysaccharides occur in the walls with different degrees of substitution of the backbone. Those populations of polysaccharides with the lowest degrees of substitution are the most likely to hydrogen bond to the cellulose microfibrils. The second network, equivalent to the network of pectic polysaccharides in the primary walls of dicotyledons, is likely to be composed of all the other non-cellulosic polysaccharides in the walls.

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