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THE CELL WALLS OF PTERIDOPHYTES AND OTHER GREEN PLANTS – A REVIEW

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ABSTRACT

The cell wall is one of the defining characteristics of plants and is a fundamental component in normal growth and development. Cell wall composition is a potentially valuable source of phylogenetic information as notable similarities and differences exist between and within major embryophyte groups. In particular, there is a pronounced chemical demarcation between the eusporangiate pteridophytes (high mannan, low tannin) and the leptosporangiate pteridophytes (low mannan, high tannin). The results of recent biochemical and immunocytochemical investigations have shown that changes in cell wall composition accompanied the bryophyte–lycopodiophyte and eusporangiate–leptosporangiate transitions.

CELL WALL FUNCTION

The earliest plants existed in an aqueous environment and their cell walls evolved in large part as one of the strategies to counteract the associated osmotic stress (Gerhart & Kirshner 1997). The cellulose-rich cell wall is one of the defining characteristics of plants, most of which now inhabit terrestrial environments. When the plant cell wall was first described by the microscopist Robert Hooke in the seventeenth century it was considered to be an inert skeleton. However, these walls are now known to have numerous biological roles, including the regulation of cell expansion, the control of tissue cohesion, defence against microbial pathogens, and ion exchange, and are a source of biologically active oligosaccharides (Goldberg *et al.*, 1994; Brett & Waldron, 1996; Cassab, 1998; Dumville & Fry, 1999; Fry 1999; Côté & Hahn, 1994; Côté *et al.*, 1998). The cell wall is a dynamic structure that is continually modified by enzyme action during growth, development, environmental stress and infection (Cassab 1998).

Stebbins (1992) suggested that changes in cell wall composition were involved in bryophyte diversification and had a role in the evolution of leptosporangiate ferns from their eusporangiate ferns ancestors. The new environmental challenges experienced during the colonization of land and those experienced during the development of the tracheophyte and leptosporangiate conditions may have driven rapid evolution of cell walls and led to the differences in wall composition between groups of extant land plants that will be discussed in this review.

TYPES OF CELL WALL

Cell walls consist of three types of layers: the middle lamella, the primary cell wall and the secondary cell wall. The middle lamella is deposited soon after mitosis and creates a boundary between the two daughter nuclei. The location of the new wall is directed,

in charophycean algae and land plants, by the phragmoplast, a cluster of microtubules (Pickett-Heaps & Northcote, 1966; Marchant & Pickett-Heaps, 1973; Brown & Lemmon, 1993). The primary cell wall, typically 0.1–10 μm thick, is deposited once the cell plate is complete and continues to be deposited whilst the cell is growing and expanding. The primary cell wall defines cell shape and thereby contributes to the structural integrity of the entire plant. At maturity some common cell types (parenchyma and collenchyma) frequently have only a primary cell wall.

The fixed, immobile nature of plant cells and tissues means that the plane of cell division and the sites of cell expansion are closely regulated and exert a strong influence on subsequent plant morphology (Fowler & Quatrano, 1997). Cellulose microfibril orientation controls the direction of cell elongation (Saxena & Brown, 2005); therefore mutations that resulted in changes in the mechanisms of early cell wall deposition, particularly those concerning cellulose, are likely to have had significant effects on plant evolution. Niklas (2005) has hypothesised lateral transfer of cellulose synthase genes across diverse prokaryotic and eukaryotic species because of similarities in cellulose synthesis mechanisms (Giddings et al., 1980; Wada and Staehelin, 1981; Murata and Wada, 1989). Control over the orientation of new cell wall divisions may exert some influence over the direction of plant growth. Light has been shown to exert control over the positioning of new cell walls in apical cells of fern gametophytes (Racusen, 2002) in such a way as to cause two dimensional growth. A plant will then exhibit an upward growth habit in addition to growing flat on the substrate. Light availability was probably an important environmental stimulus driving evolution of vertical plant growth and therefore vascular plants.

A secondary cell wall, if present, is laid down internally to the primary cell wall at the onset of differentiation, once cell growth has ceased. Secondary cell wall composition and ultrastructure in spermatophytes varies from one cell type to another as well as between plant species. This variability may reflect specific cell function. For example, many secondary cell walls, particularly xylem cells, contain lignin which increases wall strength.

CELL WALL COMPOSITION

Analytical methods used in cell wall studies

Cell wall composition has been determined using numerous analytical methods. The glycosyl residue composition of a cell wall polysaccharide is typically obtained after acid hydrolysis. The released glycoses are then identified using paper chromatography, thin-layer chromatography, high pressure liquid chromatography or gas chromatography (Fry, 2000). Numerous chemical and enzymic methods have been developed to generate oligosaccharide fragments from specific polysaccharides that can be structurally characterised by nuclear magnetic resonance spectroscopy and mass spectrometry. Immunocytological methods are becoming increasingly valuable tools for wall analysis with the increased availability of polysaccharide-specific monoclonal antibodies (Knox, 1997; Willats et al., 2000; <http://cell.cerc.uga.edu/~mao/wallmab/Antibodies/antib.htm>), and proteins that contain specific carbohydrate-binding modules (McCartney et al., 2004). Several monoclonal antibodies raised to angiosperm cell wall polysaccharides (Willats et al., 2000; Jones et al., 1997; Puhlmann et al., 1994; Freshour et al., 1996) are able to recognise at least some epitopes (structures within a molecule which are recognised by antibodies; a macromolecule may contain many distinctly different epitopes) in pteridophyte cell

walls (Figure 1) indicating that some of the structures present in angiosperm cell wall polysaccharides are conserved.

Primary cell wall polysaccharides

The primary cell wall is composed of crystalline cellulose microfibrils that are embedded in a gel-like matrix of non-cellulosic polysaccharides and glycoproteins (Fry, 2000). Current primary cell wall models depict a cellulose-hemicellulose network that is formed from cellulose microfibrils that are interconnected by hemicellulosic polysaccharides, such as xyloglucan, mixed-linkage β -glucan or arabinoxylan, forming a cellulose-hemicellulose network (Carpita & Gibeaut, 1993, Mishima et al., 1998). The cellulose-hemicellulose network coexists with a second network that consists of the pectic polysaccharides homogalacturonan, rhamnogalacturonan-I and rhamnogalacturonan-II and a further network of structural glycoproteins.

Detailed structural studies of primary cell walls have only been performed on a limited number of angiosperms and gymnosperms. Nevertheless, it is generally assumed that seed plants have primary cell walls with similar but not identical compositions. The quantitatively predominant monosaccharide present in the walls are D-glucose (Glc), D-galactose (Gal), D-mannose (Man), D-xylose (Xyl), L-arabinose (Ara), L-fucose (Fuc), L-rhamnose (Rha), and D-galacturonic acid (GalA) (Albersheim, 1976; McNeil et al, 1984; Fry, 2000). The primary cell walls of gramineous monocots typically contain more Xyl and less GalA, Gal and Fuc (Burke et al., 1974; Carpita, 1996) than other angiosperms whereas gymnosperm primary cell walls are similar in composition to those of dicotyledonous angiosperms but contain more Man residues (Edashige & Ishii, 1996, Thomas et al., 1987; Popper and Fry, 2004).

Additional variation of cell wall composition exists at the polysaccharide level. Mixed-linkage glucans appear to occur only in gramineous monocots and closely related members of the Poales (Smith & Harris, 1999). Pectic polysaccharides are major components of the primary cell walls of dicots, non-gramineous monocots, and gymnosperms. Recent studies suggest that these polysaccharides are also abundant in fern cell walls (Popper & Fry, 2004; Matsunaga et al., 2004). Xyloglucan, a hemicellulosic polysaccharide, is present in the cell walls of bryophyte gametophytes (Kremer et al. 2004), pteridophytes, lycopodiophytes, gymnosperms, and angiosperms, but has not been detected in the cell walls of charophycean green algae (Popper & Fry 2003). Similarly, hydroxyproline (Hyp), a major component of cell wall glycoproteins and proteoglycans, is present in embryophyte but not charophyte walls (Gotteli & Cleland, 1968). Thus, the appearance of xyloglucan and Hyp-rich proteins in primary cell walls is likely to have occurred after the divergence of charophytes and embryophytes from their last common ancestor (Niklas 2005).

Pteridophytes, gymnosperms and angiosperms form a well-supported monophyletic group, the tracheophytes (vascular plants) which originated approximately 420 million years ago (Judd et al., 1999). The primary cell walls of extant Pteridophytes (= non-seed vascular plants, including ferns, horsetails and club-mosses; Pryer et al., 2001) have not been studied in detail. However, there is increasing interest in the walls of non-seed plants because an understanding of the structures and functions of their walls may provide insights into the evolution and wall biology of seed plants. For example, in a recent report it was shown that pteridophyte and spermatophyte walls contain comparable amounts of the borate-ester cross-linked pectic polysaccharide referred to as rhamnogalacturonan II. The structure of rhamnogalacturonan II is conserved in the

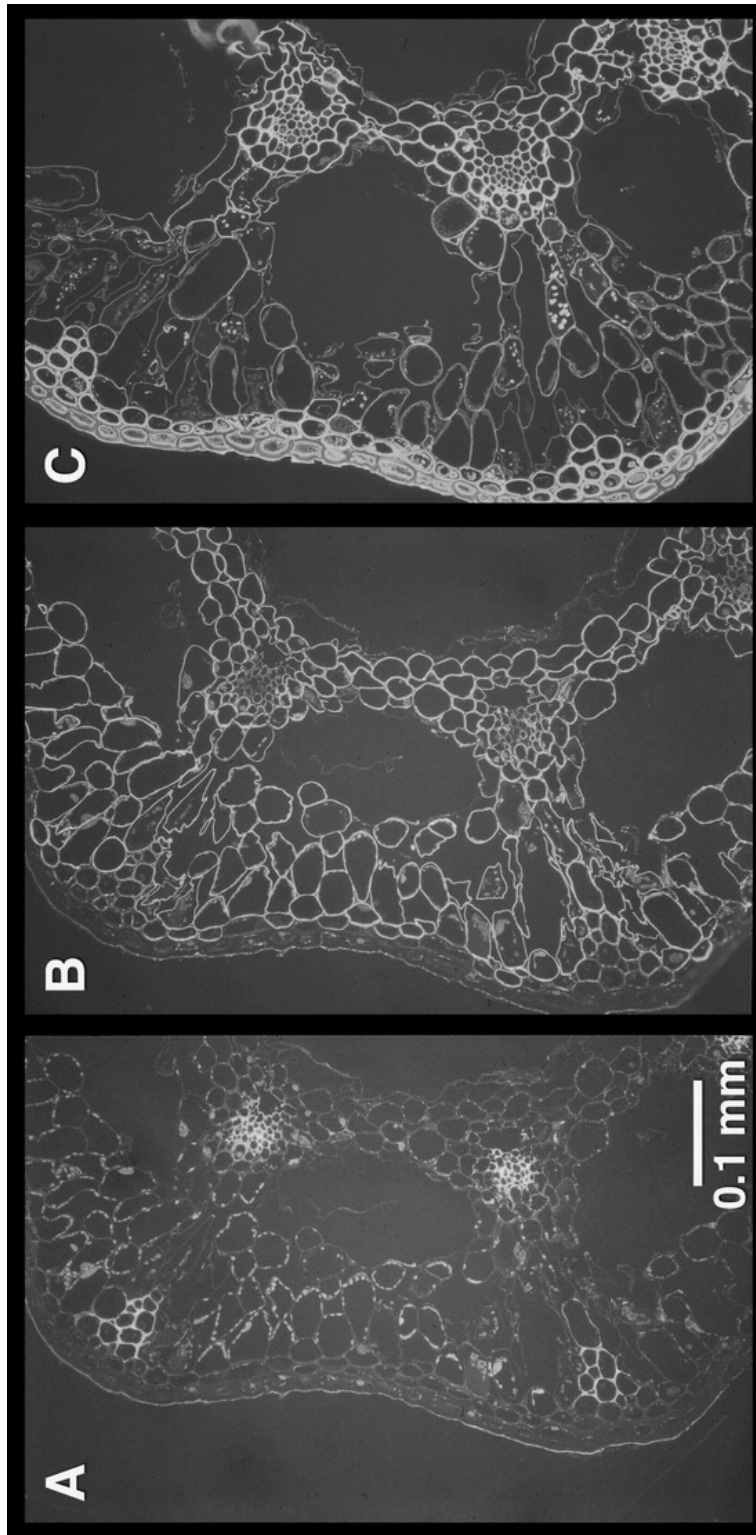


Figure 1. Transverse sections of *Equisetum* sp. stem labelled with the monoclonal antibodies. A: CCRC-M1, which recognises epitopes present in fucosylated xyloglucan; B: LM5, which recognises 1,4-linked β -D-galactan; and C: LM6, which recognises 1,5-linked α -L-arabinan.

walls of angiosperms, gymnosperms, pteridophytes and lycopodiophytes (Matsunaga et al., 2004). Conclusive evidence for the occurrence of rhamnogalacturonan II in bryophytes is lacking because none of the sugars diagnostic for this polysaccharide were detected in the walls of avascular plants (Matsunaga et al., 2004). It is therefore likely that rhamnogalacturonan II evolved in parallel with vascular plants. The conservation of rhamnogalacturonan II structure is quite remarkable since this polysaccharide contains 12 different glycoses linked together by 20 different glycosidic linkages. It is likely that rhamnogalacturonan II structure is constrained because its cross-linking involves the formation of a borate diester between two specific apiose residues. Recent studies have shown that plants carrying mutations that result in altered rhamnogalacturonan II structure have decreased borate cross-linking of rhamnogalacturonan II and exhibit growth abnormalities (O'Neill et al., 2001; Ryden et al., 2003).

Numerous morphological gaps exist between bryophytes and lycopodiophytes and lycopodiophytes and pteridophytes (Kenrick & Crane, 1997). These arise largely owing to the fact that extant pteridophytes are the surviving progeny of once diverse and ecologically dominant taxa (Raven, 1993; Kenrick & Crane, 1997). Nevertheless, many protracheophyte fossils have remnants of cell wall tracheary tissues that span some of the morphological gaps between bryophytes, lycopodiophytes and pteridophytes (Boyce et al., 2003).

Extant ferns are divided into two groups: eusporangiate (where the sporangium wall has two or more cell layers) and leptosporangiate (where the sporangium wall has just one cell layer). The majority of extant ferns belong to the monophyletic leptosporangiate group which is also defined by the presence of an annulus, a sporangial stalk, a vertical first zygotic division and a primary xylem with scalariform pits. The eusporangiate condition is generally believed to have diverged earlier and is characteristic of lycopodiophytes, equisetophytes and psilotophytes as well as ferns in the Ophioglossaceae and Marattiaceae. These ferns, are believed to be among the earliest diverging (Smith 1995, Pryer et al. 1995).

Differences in cell wall composition correlate with emergence of the tracheophytes and divergence of the pteridophytes. Divergence of leptosporangiate and eusporangiate ferns is associated with a decrease in the amounts of mannose in the primary cell wall (Popper & Fry, 2004). Eusporangiate pteridophyte and bryophyte primary cell walls typically contain more mannose than the primary cell walls of leptosporangiate pteridophytes (Popper & Fry, 2003 & 2004). Moreover, proanthocyanidins are associated with primary cell walls from leptosporangiate ferns, gymnosperms and angiosperms, but not eusporangiate pteridophytes (Popper & Fry 2004; Bate-Smith & Learner, 1954). Leptosporangiate ferns are the earliest diverging plants in which proanthocyanidins start to predominate over flavonols (De Bruyne et al., 1999). It is likely that the production of proanthocyanidins evolved at the same time as the leptosporangiate condition rather than the vascular condition because proanthocyanidins remain important in early diverging angiosperms but their synthesis decreases in more advanced orders. Leptosporangiate ferns appear to have diversified in an environment dominated by seed plants and may therefore have faced selective pressures similar to those experienced by seed plants (Schneider et al., 2004). This may explain why the primary cell walls of leptosporangiate ferns, including *Osmunda*, one of the earliest diverging extant leptosporangiate ferns (Pryer et al., 2001; Schneider et al., 2004), are more similar to those of seed plants than to those of eusporangiate

pteridophytes. Table 1 summarises the differences in cell wall composition found between different land plants.

The lycopodiophytes form a distinctive, basal, monophyletic clade within the eutracheophytes and evolved during the Devonian (408–360 million years ago) (Bateman et al. 1998). The seldom observed monosaccharide residue, 3-*O*-methylgalactose (3-*O*-MeGal) is a quantitatively major component of homosporous and heterosporous lycopodiophytes primary cell walls (Popper & Fry, 2001). It is likely that 3-*O*-MeGal is a component of many lycopodiophyte primary cell wall polysaccharides (including xyloglucan (Malcolm O'Neill, personal communication)). The occurrence of this sugar may support the claim of monophyly of lycopodiophytes since little if any 3-*O*-MeGal is present in the primary cell walls of other land plants investigated (Popper & Fry, 2001). The divergence of the lycopodiophytes and the subsequent divergence of the extant homosporous and heterosporous clades appear however to be associated with a decrease in the amounts of *O*-methylated sugar residues. Small amounts of 3-*O*-Methylrhamnose (3-*O*-MeRha; trivial name acofriose) have been detected in the primary cell walls of charophytes, bryophytes, pteridophytes and gymnosperms (Popper & Fry, 2003; Matsunaga et al., 2004; Akiyama et al., 1988; Anderson & Munro, 1969). Matsunaga et al., (2004) demonstrated that this monosaccharide was present as a component of rhamnogalacturonan II isolated from several pteridophytes. However, no 3-*O*-MeRha has been detected in angiosperm primary cell walls, showing that the ability to synthesise this *O*-methylated sugar is not required for land plant survival. The existence of 3-*O*-meRha in a wide range of diverse plants could be explained by the rapid divergence of lineages that occurred during the emergence of the euphyllophytes (Pryer et al., 2001).

Secondary cell wall polysaccharides

Xylans are the quantitatively major cellulose-linking polysaccharides in higher plant secondary cell walls. Typical angiosperm and gymnosperm xylans consist of a 1→4-linked β-D-xylopyranose backbone with a single α-glucuronic acid or 4-*O*-methyl-α-D-glucuronic acid residue attached to the O-2 position of the xylose residues (Shatalov et al., 1999). Xylans with a similar structure have been isolated from secondary cell walls of *Osmunda cinnamomea* (Timell, 1962).

Immunocytological studies using the monoclonal antibodies LM 10 and LM11 that recognise epitopes on xylans have shown that these polysaccharides are present in the secondary cell walls of vascular and mechanical tissues in all extant tracheophytes investigated (McCartney et al., 2005; Carafa et al., 2005). Epitopes recognized by LM11 (substituted xylans and arabinoxylans) are present in specific cell-wall layers in hornwort pseudoelators and spores (Carafa et al., 2005) but the epitopes recognized by LM10 (unsubstituted (1→4)-β-xylans) were absent (Carafa et al., 2005). LM10 and LM11 did not bind to liverwort and moss cell walls (Carafa et al., 2005), suggesting that no detectable amounts of xylan are in the thickened cell walls of these bryophyte groups. The ubiquitous occurrence of xylans in tracheophytes indicates that xylans may have provided a pre-adaptive advantage, occurring in protracheophytes, allowing the evolution of highly efficient vascular and mechanical tissues and enabling the tracheophytes to develop a larger size and to colonize water-limited environments (Bateman et al., 1998). The immunocytological studies of Carafa et al. (2005) suggest that hornworts may be sister to the tracheophytes.

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Table 1: Composition of land plant cell walls.

Plant Group	Monosaccharides		Polysaccharides					Other
	3-O-MeRha	3-O-MeGal	Xylan	Mannan	Xyloglucan	Rhamnogalacturonan II	Pectin	
Charophytes	+	-	-	+	-	±	++	-
Hornwort	+	-	+	+	+	±	+++	-
Liverworts and basal mosses	+	-	-	+	+	±	++	-
Advanced mosses	+	-	-	+	+	±	++	-
Homosporous lycopodiophytes	+	+	+	+	+	+	+	-
Heterosporous lycopodiophytes	-	+	+	+	+	+	+	-
Eusporangiate ferns	-	±	+	+	+	+	+	-
Leptosporangiate ferns	-	±	+	±	+	+	+	+
Spermatophytes	-	±	+	±	+	+	+	+

-, Not detectable; ±, trace; + present at low concentration; ++, present at moderate concentration; +++, present at high concentration.

The backbones of galactoglucomannans are composed of alternating (1→4)-linked β -D-mannopyranose and β -D-glucopyranose residues. Some of the mannose is substituted at O-6 by α -D-galactopyranose or β -D-galactopyranose-(1, 2)- α -D-galactopyranose side chains. Galactoglucomannans are major components of the cell walls of the woody tissues of both angiosperms and gymnosperms, and are minor components in the primary cell walls of angiosperm and gymnosperm cambial tissues, in suspension-cultured tobacco cells (Eda et al. 1985), and in secondary cell walls from the stem tissues of the aquatic moss *Fontinalis antipyretica* (Geddes & Wilkie 1971, 1972) and the fern *Pteridium aquilinum* (Bremner & Wilkie 1971). The solid-state ^{13}C NMR spectra of fibrous material of the silver tree fern, *Cyathea dealbata* contain a weak signal at 102 ppm that may originate from C-1 of a mannose residue in a glucomannan or a mannan (Newman, 1997). The occurrence of galactoglucomannans in secondary cell wall tissues, including those of bryophytes, indicates galactoglucomannans evolved prior to the divergence of tracheophytes. Galactoglucomannans may have played an important role in providing tensile strength in bryophyte secondary cell walls.

Cell wall composition in relation to plant phylogeny

Major transitions in cell wall diversity were mapped against the phylogeny of Kenrick and Crane (1997; Figure 2) because this phylogeny is one of most comprehensive treatments of plant taxa and their closest extant common ancestors, the charophycean green algae. The phylogeny proposed by Pryer et al. (2001) is based on vegetative and reproductive morphological/anatomical characters in addition to plastid (*atpB*, *rbcL* and *rps4*) and nuclear (small subunit) DNA sequence data. Pryer et al. (2001) place the bryophytes as basal but the relationships to each other and to vascular plants remain unresolved whereas Kenrick and Crane (1997) suggest liverworts to be the earliest evolving among land plants. On the basis of cell wall characters, hornworts may be basal among bryophytes as they (and possibly some charophycean green algae) contain the unusual disaccharide α -D-glucuronosyl-(1→3)-L-galactose (Popper et al., 2003). Cell walls of hornwort also have a high concentration of glucuronic acid; the concentration of glucuronic acid in cell walls of liverworts and mosses is lower than that in hornworts but greater than that of vascular plants (Popper et al., 2003). However, cell wall characters also suggest a close relationship between hornworts and tracheophytes. Immunocytological studies by Carafa et al. (2005) show hornworts to be the only bryophytes to contain substituted xylans and arabinoxylans. Among extant taxa, substituted xylans and arabinoxylans are found predominantly within the tracheophytes (Carafa et al., 2005). Mapping further cell wall related characters onto the phylogeny generated by Pryer et al. (2001) shows that cell wall characters partially support the three tracheophyte divisions suggested namely (1) lycopodiophytes, (2) seeds plants and (3) a group consisting of equisetophytes, psilotophytes, eusporangiate and leptosporangiate ferns. Pteridophyte cell walls, in common with lycopodiophytes, differ from spermatophytes in being mannose-rich. Lycopodiophytes are supported as being monophyletic primarily by the presence of 3-O-methylgalactose which is absent or present at much lower concentration in other tracheophytes. However, spermatophyte and filicophyte cell wall preparations are both associated with tannins (Popper and Fry, 2004) which would split the group containing equisetophytes, psilotophytes, eusporangiate and leptosporangiate ferns proposed by Pryer et al. (2001). However, the acquisition of tannins may be homoplastic having evolved at the same

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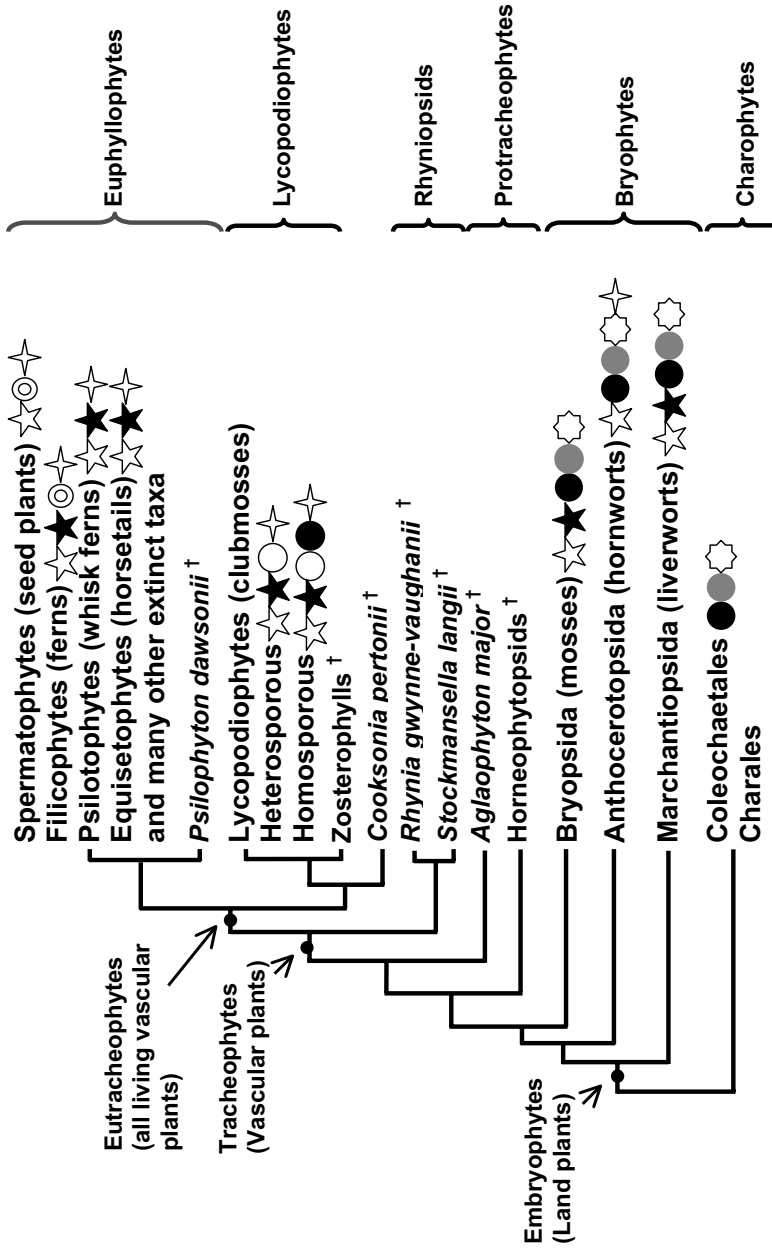


Figure 2. Land plant phylogeny as present by Kenrick and Crane (1987) annotated to show major transitions in cell wall components. The presence of specific cell wall components are shown as follows; xyloglucan, x; mannose, M; 3-O-methylgalactose, 3-O-MGal; Tannin, T; branched 4-linked xylan, xyl; GlcA, GlcA. Extinct plants, indicated by †, which represent large gaps in plant morphology are included.

time within the spermatophyte and filicophyte groups due to a common selection pressure. Schneider et al. (2004) suggest polypod ferns diversified (~ 180 million years ago) subsequent to radiation of the angiosperms (~250 million years ago). Evidence from cell wall characters is therefore seen in general to partially corroborate an hypothesised early mid-Devonian split within the euphyllophytes and subsequent concurrent evolution of seed plants and pteridophytes.

Cell wall enzymes

A complete description of the enzymes involved in plant cell wall biosynthesis and modification has not been obtained and few of the membrane-bound polysaccharide synthases have been biochemically characterised (Burton et al. 2000). I will briefly discuss some enzyme families (Csl, Cesa and XTH) whose function has been at least partially elucidated.

Cellulose is one of the most abundant organic molecules on the planet with plants synthesising more than 10^{11} metric tons per year (Hess et al., 1928). Proteins that have a role in cellulose synthesis are encoded by a large family of cellulose synthase genes (Cesa). All members of the Cesa gene family isolated from land plants encode for integral membrane proteins which share many conserved regions (Richmond & Somerville, 2000; Vergara & Carpita, 2001) and have some molecular motifs identical to those found in Cesa proteins from the green alga *Mesotanium caldariorum* (Roberts et al., 2001; Roberts & Roberts, 2004). Genes within the Cesa family are thought to be functionally non-redundant owing to the arrangement of the proteins they encode in structurally well-defined transmembrane complexes (Kimura et al., 1999). A gene superfamily known as cellulose synthase-like (Csl) genes has also been described (Richmond & Somerville, 2000). Proteins encoded by these genes are likely to be involved in the synthesis of hemicellulosic polysaccharides including xyloglucan, xylan and glucomannan (Leipman et al., 2005; Dhugga et al., 2005).

Xyloglucan endotransglycosylases/hydrolases (XTH's) are a class of enzymes that transglycosylate xyloglucan. XTH's are encoded by at least 33 genes in *Arabidopsis* and recent studies have revealed that individual members of this gene family exhibit specific temporal and spatial expression patterns (Matsui et al., 1995). Two loss-of-function *Arabidopsis* mutants of the AtXTH27 gene (XTH27-1 and XTH27-2) have short tracheary elements in the tertiary veins and a reduced number of tertiary veins in the first leaf. The highest level of AtXTH27 mRNA expression was seen during leaf expansion where the tracheary elements were elongating. The AtXTH27 gene therefore appears to have a role in cell wall modification during development of tracheary elements (Matsui et al., 1995). Vissenberg et al. (2003) have shown that the primary cell walls of lycopodiophytes, early diverging pteridophytes and the earliest diverging extant vascular plants (Raubeson and Jansen, 1992; Manhart, 1994, 1995; Pryer et al., 1995; Wolf, 1997; Duff and Nickrent, 1999) contain XTH activity. Owing to the control of tracheary element elongation by an XTH and because XTH activity has been detected in sporophyte and gametophyte tissues from the liverwort *Marchantia* and in gametophyte tissue from a moss, *Mnium* (Fry et al., 1992) it is likely that divergence of the XTH genes played a role in the evolution of vascular plants.

The existence of multiple members of Csl, Cesa, and XTH gene families allows for temporal and spatial differences in gene expression and may account for differences in cell wall polysaccharide composition and morphologies among various plant groups and between different tissues within the same plant.

Cell wall-associated proteins

Cell wall-associated proteins may directly influence plant morphogenesis. Morphogenesis in plants is the result of differential growth of the organs at the level of cell walls (Kaplan & Hageman 1991). The cell wall-associated proteins known as arabinogalactan proteins have a diverse range of structures and functions. In large part, heterogeneity found in arabinogalactan proteins is within the carbohydrate domain (Gaspar et al., 2001). This diversity may allow for subtle differences in function. Much of the evidence relating to arabinogalactan distribution and function has been based on the use of monoclonal antibodies which react with carbohydrate epitopes within arabinogalactan proteins (McCabe et al., 1997; Casero et al., 1998). Arabinogalactan proteins are thought to play a major role in cell-cell interactions and have been shown to have a morpho-regulatory role in bryophyte (Basile 1980, Basile & Basile 1983, 1987) and higher plant (Kreuger & van Holst 1996, Majewska-Sawka & Nothnagel, 2000, Johnson et al., 2003) development. Arabinogalactan proteins are synthesised by the moss *Physcomitrella patens*, where they appear to have a role in regulating the extension of protonemal cells with apical tip growth (Lee et al., 2005). Thus, arabinogalactan proteins, and in particular their carbohydrate domain, may be important agents defining different body-plans of all land plants and thus pivotal in the evolution of the major groups of land plants.

Expansins are wall proteins encoded by a multigene family. These proteins modify the mechanical properties of cell walls, allowing turgor-driven cell enlargement (Cosgrove, 2000). There are two subfamilies of expansins, α and β . The α -expansins have a highly conserved protein sequence and are found in all embryophyte taxa (land plant groups) including the aquatic ferns, *Marsilea* and *Regnellidium* (Kim et al., 2000) and the moss *Physcomitrella patens* (Li et al., 2002) whereas β -expansins are present in low concentration in dicotyledonous angiosperms and occur at a much higher concentration in members of the monocotyledonous Poales (Cosgrove, 2000). Expansins are believed have a prominent role in xylem development (Cosgrove, 2000) and thus their evolution may be closely associated with that of tracheophytes.

ECOLOGICAL CONSEQUENCES OF CELL WALL DIVERSITY

Variation in cell wall composition influences which pathogens can infect a plant. Cell walls are a physical barrier to bacterial, viral and fungal pathogens. However, many pathogens secrete enzymes that degrade cell wall components, those which degrade polysaccharides being among the most specific. Most glycanases can only cleave the glycosidic linkage between two specific monosaccharides and often that bond must be between two particular carbon atoms and of a specific anomeric configuration. For example, endopolygalacturonases can only cleave the glycosidic bond between 1, 4-linked α -D-galacturonic acid residues. Thus, changing the type of glycosidic bond may alter the susceptibility of a polysaccharide to enzyme hydrolysis (Albersheim et al., 1969). Cell wall composition is therefore likely to be a factor that determines which fungi and bacteria are able to be pathogenic to particular plants.

Decomposers synthesise specific cell wall-degrading enzymes. Not all saprophytes will be able to synthesise every enzyme required to degrade all the polysaccharides in a cell wall. Thus, saprophytes tend to work synergistically to degrade plant material. Differences in cell wall biochemistry between a fern-rich as opposed to an angiosperm or gymnosperm-rich community may be reflected by differences in the decomposers

acting on the plant materials present. Therefore, cell wall biochemistry may be an important factor determining fungal and bacterial biodiversity.

CONCLUSIONS

The transition from an aqueous to an initially low-competition gaseous medium exposed plants to new physical conditions and resulted in selection for key physiological and structural changes. Early plant terrestrialisation is predicted to have rapidly filled all niches where water availability was limited (Bateman et al. 1998), thereby increasing competition and driving selection for turgor-stabilised upright stems and decreased dependence on water availability. Mutations that enabled plants to adopt a more upright growth habit, many of which are likely to have been cell wall related, would have been strongly favoured. It is likely that these evolutionary pressures brought about the differences in cell wall composition that occurred during the colonisation of land and during the emergence of the vascular and leptosporangiate conditions. Major differences in cell wall composition between different plant taxa are summarised in figure 2. Differences appear to provide specific traits that appear to be landmarks. Specifically, the presence of the primary cell wall polysaccharide, xyloglucan, in all land plants, but apparent absence from their closest extant common ancestors, the charophycean green algae (Popper & Fry, 2003), implies that xyloglucan may have been required for land colonisation or that the subsequent evolution of land plants required walls that contained xyloglucan. Attainment of the vascular condition is associated in secondary cell walls with a reduction in total primary cell wall uronic acid content (Popper & Fry, 2003 and 2004) and the presence of highly substituted xylans (Carafa et al., 2005). Complex xylans also occur in hornwort cell walls which, contrary to the phylogeny presented in figure 2 (Kenrick & Crane, 1997), may suggest that tracheophytes are more closely related to hornworts than they are to liverworts and mosses. Vascular plants are unified by the presence of rhamnogalacturonan II in their primary cell walls (Matsunaga et al., 2004). Rhamnogalacturonan II and the acquisition of a boron-dependant growth habit together with branched xylans are likely to have been important in evolution of upright stem tissues. Among vascular plants, there is a pronounced chemical demarcation between eusporangiate pteridophytes (high mannan, low tannin) and leptosporangiate ferns (low mannan, high tannin) (Popper & Fry, 2004). The emergence and divergence of the pteridophytes appears, therefore, to be associated with a period of modification in cell wall composition.

Stebbins (1992) has stated that 'even the most superficial survey of ecological plant anatomy points to the adaptive importance of cell wall differentiation'. Indeed, the present literature shows changes in cell wall polysaccharide composition and expression of cell wall proteins and enzymes are likely to have been fundamental to the emergence, divergence and survival of extant ferns.

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