The genome sequence of the moss Physcomitrella patens has stimulated new research examining the cell wall polysaccharides of mosses and the glycosyl transferases that synthesize them as a means to understand fundamental processes of cell wall biosynthesis and plant cell wall evolution. The cell walls of mosses and vascular plants are composed of the same classes of polysaccharides, but with differences in side chain composition and structure. Similarly, the genomes of P. patens and angiosperms encode the same families of cell wall glycosyl transferases, yet, in many cases these families have diversified independently in each lineage. Our understanding of land plant evolution could be enhanced by more complete knowledge of the relationships among glycosyl transferase functional diversification, cell wall structural and biochemical specialization, and the roles of cell walls in plant adaptation. As a foundation for these studies, we review the features of P. patens as an experimental system, analyses of cell wall composition in various moss species, recent studies that elucidate the structure and biosynthesis of cell wall polysaccharides in P. patens, and phylogenetic analysis of P. patens genes potentially involved in cell wall biosynthesis.

Keywords: cell wall, polysaccharide, cellulose, cellulose synthesis complex, glycosyl transferase, moss, Physcomitrella patens

MOSS BIOLOGY AND EVOLUTION

The common ancestor of land plants is believed to have resembled extant mosses in having a biphasic life cycle with a dominant haploid gametophyte and rudimentary adaptations for tolerating the aerial environment. Because they have retained these characteristics, mosses are often referred to as “lower” plants (Mishler and Oliver, 2009). Despite this designation, mosses are highly successful, comprising more than 10,000 species adapted to diverse habitats ranging from submerged aquatic to desert (Buck and Goffinet, 2000). Mosses differ from vascular plants in the strategy they employ to survive in the dry aerial environment. Vascular plants are homeohydric with a thick cuticle to reduce dehydration, roots to extract water from the soil, and vascular tissue to distribute water internally. In contrast, mosses are poikilohydric, depending on a surface film of free water to maintain hydration. Although some mosses are confined to aquatic habitats, many are dehydration tolerant and some are desiccation tolerant (Mishler and Oliver, 2009).

The life cycle, morphology, and biochemistry of mosses have been influenced by selective pressure associated with poikilohydry. Because cellular water status is controlled by surface absorption and diffusion, moss organs are small and thin, and lignin is not required to provide support against gravity or the negative pressures generated during transpiration (Mishler and Oliver, 2009). In most mosses, haploid spores produce protonemal filaments that extend by apical division and tip growth (Figure 1). The filaments produce buds that develop into leafy gametophores, which enlarge by diffuse growth. Haploid spores are produced by diploid sporophytes, which develop from eggs fertilized by swimming sperm at the gametophore apex (Schumaker and Dietrich, 1998).

Although structurally simple, moss gametophytes contain different cell types. The protonema is differentiated into chloroplast-rich chloronemal cells and caudonemal cells, which elongate three times faster (Menand et al., 2007). In response to dehydration stress, protonemal cells resume division and differentiate into thick-walled, dehydration-tolerant brachycyttes, and subbending stomata cells, which undergo programmed cell death (Decker et al., 2006). Gametophores include a stem, leaves, axillary hairs, and rhizoids. The stem typically consists of small, thick-walled epidermal and subepidermal cells, thin-walled parenchyma cells, and conducting cells. The conducting cells include hydroids and leptoids, which are functionally analogous to xylem and phloem (Buck and Goffinet, 2000). Similar to tracheary elements, hydroids are dead at maturity and connected by perforations, but they lack thick lignified secondary cell walls (Hebant, 1977). Leaves are typically one cell layer thick except for the midribs and margins, which may consist of multiple layers of differentiated cells. Leaf cells of Sphagnum species include photosynthetic chlorocytes and hyaloocytes with elaborate cell wall thickenings. Other leaf cell specializations include papillae and various surface elaborations. Additional differentiated cell types form the gametangia, gametes, and sterile paraphyses. The sporophyte stalk, sporangium, and spores also consist of specialized cell types (Buck and Goffinet, 2000), including stomata (Sack and Paolillo, 1983).
Although mosses share a poikilohydric ecological strategy and common body plan, their diversification and colonization of different habitats have been accompanied by the evolution of specialized morphological and biochemical adaptations that must be considered when inferring evolutionary trends from comparative studies of mosses and vascular plants. The mosses diverged from the land plant lineage between the liverworts and the hornworts, which most recent phylogenies place as sister to the vascular plants. The moss lineage includes the “true mosses” and three early divergent and ecologically specialized lineages, the aquatic Sphagnales, the desiccation-tolerant rock-dwelling Andreales, and the morphologically diverse Polytricales (Mishler and Oliver, 2009). Whereas mosses have retained primitive aspects of cell wall structure and composition due to poikilohydr, they have also evolved special cell wall adaptations that enabled them to colonize diverse habitats.

**Physcomitrella patens**, the Model Moss Species

As a member of the Funariales, *Physcomitrella patens* occupies a phylogenetic position at the base of the true mosses. As an inhabitant of moist soils that tolerates dehydration, but not desiccation, it represents a “primitive moss ecology” (Mishler and Oliver, 2009). This lack of specialization for extreme conditions combined with abundant genomic resources (Rensing et al., 2008), efficient production of transgenic genotypes, and ease of culture and experimental manipulation (Cove, 2005) provides an opportunity to relate the diversification of gene families to innovations in cell wall composition, structure, and development that accompanied the adaptation of plants to life on land. Other advantages of *P. patens* include the ability to produce large amounts of tissue consisting of a single cell type (chloronemal filaments) and rapid cell wall regeneration in protoplasts (Lee et al., 2005a; Lawton and Saidasan, 2011; Roberts et al., 2011).
CELL WALL ANALYSIS

Cell wall polysaccharide composition has been investigated in several moss species, including Physcomitrella patens. As a complement to biochemical methods, immunological and affinity approaches employing antibodies and carbohydrate binding modules that recognize a variety of cell wall polysaccharides (Knoopp, 2008) have been used to examine the distribution of polysaccharides and with the microarray method known as comprehensive microarray polymer profiling (CoMPP; Moller et al., 2007).

CELLULOSE

Cellulose exists in the cell walls of all mosses that have been examined. It was detected in P. patens by CoMPP, sugar linkage analysis, and staining with Timosyl and CBM3A, a probe specific for crystalline cellulose (Krener et al., 2004; Lee et al., 2005b, 2011; Moller et al., 2007; Nothnagel and Nothnagel, 2007; Goss et al., 2012). It is typical for cellulose, 5–20 nm wide microfibrils are visible in extracted and shadowed cell walls (Figure 2A). Microfibril impressions also occur in freeze-fractured plasma membranes (Figure 2B). Fibrils detected by atomic force microscopy on the surface of air-dried protonemal filaments were 250 nm in diameter (Wray et al., 2008), which is consistent with cellulose aggregation upon drying.

The P. patens genome includes seven Cellulose Synthase genes (PpCESA3, -4, -5, -6, -7, -8, and -10 = -11) and three CESA pseudogenes (PpCESA1, -2, and -9; Roberts andBushoven, 2007; Yin et al., 2009; Wise et al., 2011). Whereas seed plant CESAs are specialized for primary and secondary cell wall deposition, the CESAs of P. patens may be specialized for tip and diffuse growth. PpCESA5 is required for leafy gametophore morphogenesis and is upregulated by cytokinin, which also induces gametophore development (Goss et al., 2012). Based on over-representation in EST libraries, cytokinin may also be involved in gametophore development. In contrast, PpCES6 is expressed in tip-growing protoplasts, rhizoids, and axillary hairs (Wise et al., 2011). Knockout mutants of PpCES6 and -7, which differ by three amino acids, have no morphological phenotype. Shorter gametophores were observed in one PpCES6/6 double mutant line (Wise et al., 2011). Analysis of additional PpCESA knockout mutants will be required to fully understand CESA diversification and functional specialization in P. patens.

Mosses including Funaria hygrometrica (Reiss et al., 1984; Rudolph and Schneid, 1988; Rudolph et al., 1989) and P. patens have rosette-type cellulose synthesis complexes (CSCs). CSCs are abundant near apical cell tips, some apparently emerging from secretory vesicles (Figures 2C,D), and adjacent to forming cell plates (Figure 2E). Rosette-type CSCs of seed plants contain three CESA isoforms, and it has been suggested that CESA diversification was a prerequisite for rosette CSC evolution (Doblin et al., 2002). However, phylogenetic analyses indicate that the PpCESAs are not orthologs of the functionally specialized seed plant CESAs and that the common ancestor of mosses and seed plants had a single CESA locus for the CSCs (Tanaka et al., 2003; Djerbi et al., 2005; Nairn and Haselkorn, 2005; Ranik and Myburg, 2006; Roberts and Bushoven, 2007; Kumar et al., 2009; Carroll and Specht, 2011). This implies that hetero-oligomeric CSCs evolved independently in mosses and seed plants. Published CESA phylogenies indicate that the divergence that produced primary and secondary cell wall CESAs preceded the diversification that resulted in hetero-oligomeric CSCs (Tanaka et al., 2003; Djerbi et al., 2005; Nairn and Haselkorn, 2005; Ranik and Myburg, 2006; Roberts and Bushoven, 2007; Kumar et al., 2009; Carroll and Specht, 2011). This implies that hetero-oligomeric CSCs evolved independently from homo-oligomeric primary and secondary CSCs. Although this scenario seems unparsimonious, the theory of constructive neutral evolution recently demonstrated for the V-ATPase complex in yeast (Doudittle, 2012; Finnigan et al., 2012) postulates that multisubunit complexes, such as CSCs, are driven towards a hetero-oligomeric state. Like CSCs, the transmembrane ring of yeast V-ATPase consists of three paralogous, but non-interchangeable, protein subunits. By reconstructing the common ancestor of two of these subunits and reintroducing historical mutations, Finnigan et al. (2012) showed that a gene duplication followed by complementary loss of specific interfaces involved in protein–protein interactions was responsible for the evolution of subunits that differ only in the
positions that they occupy within the complex. In this process, a high-probability loss-of-function (i.e., the inability to inter-
act with like subunits) is initially independent of selection, but
the hetero-oligomeric condition becomes locked by selection as
mutations accumulate. This driving of multimeric protein
complexes toward increased complexity explains how the hetero-
oligomeric state could have evolved independently in primary
and secondary cell wall CSCs in seed plants and, possibly, in
P. patens.

**CROSS-LINKING GLYCANS**

Xyloglucan has been detected in various moss species by the pres-
ence of isopimeroxere in driselae digest (Popper and Fry, 2003)
and in P. patens by CoMPP using antibodies directed against
non-fucosylated xyloglucan (Moller et al., 2007). Detailed struc-
tural analysis confirmed the absence of fucopyranosyl residues
and revealed that P. patens xyloglucan has an XGGG branching
pattern and novel branched side chains containing galactosy-
luronic acid and arabinoxyranosyl residues (Peta et al., 2008).
Based on immunolabeling the leaves and stems are enriched in
xyloglucan (Kulkarni et al., 2012). The five members of the P. patens CSE family of putative xyloglucan syntheses
(Cocuron et al., 2007) form a clade separate from seed plant
CSEs (Roberts and Bushoven, 2007). The P. patens genome also
encodes putative homologs of the Arabidopsis xyloglucan xyosyl
transferases XXT1 and XXT2, and galactosyl transferases MUR3
and GT18 (Peta et al., 2008). Because fucopyranosyl residues of
P. patens xyloglucan are substituted with galactosyluronic
acid or arabinoxyranosyl residues instead of galactopyranosyl
residues, it was suggested that the P. patens homologs differ
from MUR/GT18 in substrate specificity (Petén et al., 2008).
Although the P. patens genome encodes several members of GT37,
which includes the Arabidopsis xyloglucan fucosyl transferase
FUT1, sequence similarity is low (Petén et al., 2008) and the
P. patens sequences are not in the FUT1 subclade (Del Bem and
Vincente, 2010), consistent with the lack of xyloglucan fucosyla-
tion. Differences in side chain frequency in xyloglucans extracted
from protonemal and gametophore cell walls may be related to
the roles of xyloglucan in tip and diffuse growth (Petén et al.,
2008).

Mannans are present in walls of various bryophytes based on
chemical analysis (Greddes and Wilkie, 1971; Popper and Fry,
2003) and in P. patens based on CoMPP, chemical analysis, and
immunolabeling (Liepmann et al., 2007; Moller et al., 2007; Noth-
agel and Nothagel, 2007; Lee et al., 2011). The P. patens genome
includes three CSEL families (Roberts and Bushoven, 2007), at least
two of which have mannnan/glucomannan synthase activity when
expressed in insect cells (Liepmann et al., 2007).

A recent immunolabeling study failed to detect xylan-specific epitopes in eight moss species, including E. hygrometrica (Carafa
et al., 2005). However, xylan-specific epitopes were detected in
P. patens by CoMPP and sugar linkage analysis confirmed the
presence of β-1,4-linked xylan (Moller et al., 2007). A detailed
structural analysis revealed glucuronoxylan with a 1,4-linked β-
D-glucosyluronic acid and a-1,4-galacturonic acid side chains,
but no 4-O-methyl-D-glucuronic acid side chains, indi-
cating that O-methylation of glucuronic acid evolved after
divergence of mosses and vascular plants. The P. patens xylan is
also unusual in having pairs of side chains separated by a sin-
gle xylosyl residue and possibly an unidentified pentosyl residue.
Xylans from both seedless vascular plants and P. patens lack
the reducing-end sequence characteristic of seed plant xylans
(Kulkarni et al., 2012). Xylan has been immunolocalized in leaf
cells and axillary hairs in P. patens, but little or none was
detected in the stems and protoxenom filaments (Kulkarni et al.,
2012). Xylan backbone synthesis in Arabidopsis involves mem-
bers of GT43 (IRX-9, IRX-9L, IRX-14, IRX-14L) and GT47
(IRX-10, IRX-10L). The major clades containing these pro-
teins and their putative seed plant orthologs include P. patens
sequences (Kulkarni et al., 2012). However, the P. patens mem-
ers of the BX-WIRX-9L clade may not be their direct orthologs.

**PECTINS**

Pectin epitopes, including homogalacturonan, β-1,4-galactan, and
α-1,5-arabinan were detected by CoMPP and sugar linkage anal-
ysis in P. patens cell walls (Moller et al., 2007). Detergent pectin
and RG-I were also detected by immunofluorescence in leaves and
stems of P. patens (Kulkarni et al., 2012). Water conducting cells
of several species and hyaline cells from Sphagnum label preferen-
tially with antibodies directed at the arabinosylated β-1,4-galactan
epitope of RG-I (Ligrone et al., 2002; Kremer et al., 2004). The cell
walls of some moss species may contain an RG-II-like polysaccha-
ride based on the presence of 2-methyl-fucose and 2-methyl-xylose
(apiso and aceric acid were not detected) and release of cross-
linked borate by driselae (Matushaga et al., 2004). However, the

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Roberts et al. Moss cell walls

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AGPs were identified in a
Abel, W. O., Knebel, W., Koop, H.,
cans contain unusual terminal 3-
P. patens (Lee et al., 2005a, b; Moller et al., 2007).
Buck, W. R., and Goffinet, B. (2000).
Budke, J. M., Goffinet, B., and Jones,
analysis of cell wall protein genes in
P. patens ing a classical AGP, three AG peptides, and two fasciculin-like
typical of angiosperm AGPs (Fu et al., 2007). Genes encod-
arabinofuranosyl and (1,4)-linked glucuronopyranosyl residues
in addition to the (1,3,6)-linked galactopyranosyl, terminal
arabinofuranosyl and (1,4)-linked glucuronopyranosyl residues
typical of angiosperm AGPs (Fu et al., 2007). Genes encod-
ing a classical AGP, three AG peptides, and two fasciculin-like AGPs were identified in a P. patens EST database (Lee et al., 2005b) and an AGP was among the proteins identified in a proteomic analysis of dehydration response (Cai et al., 2012).
Extensis was weakly detected in P. patens by CoMP. Genome searches identified homology of GT77 proteins implicated in
extensis glycosylation (Harholt et al., 2012), but not extensis itself (Lawton and Saidas, 2011). However, a comprehensive analysis of cell wall protein genes in P. patens has not been reported.

CALLUS
Callus has been detected in mosses, including P. patens, by ar
cline blue cytochemistry (Scherp et al., 2001; Tang, 2007; Schuette et al., 2009) and CoMP (Moller et al., 2007). As in other plants and algae, callus is involved in normal developmental processes, including cytokinesis (Scherp et al., 2001) and spore formation (Schuette et al., 2009), and it also forms in response to wounding (Abel et al., 1989; Schuette et al., 2001; Tang, 2007). The association of callus with different developmental stages and stimuli is not unexpected since the P. patens genome contains 12 putative Callus

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Synthase (CalS) genes that cluster in three clades with Arabidopsis CalS genes (Schuette et al., 2009).
LIGNIN
Most reports of lignin in mosses have not withstood further scrutiny (Wong and Chapple, 2010; Espiñeira et al., 2011). How-
ever, the presence of lignin-like compounds in mosses is consistent with identification of P. patens homologs of genes encoding lignin biosynthesis enzymes (Xu et al., 2009).
CUTICLE
Although the protonemal filaments of mosses apparently lack cuticles, a hydrophobic cuticle-like layer has been reported in some moss gametophores and sporophytes (Cook and Graham, 1998; Budke et al., 2011). Although some authors have indi-
cated that P. patens gametophores lack a cuticle (Liènard et al., 2008), other histochemical studies have suggested that a cuticle is present (Wyatt et al., 2008) in this species. No analysis of P. patens genes potentially involved in cuticle biosynthesis has been reported.
PROSPECTS

While detailed structures of P. patens cell wall polysaccharides are now being revealed, few of the P. patens glycosyl transferases have been characterized functionally. Further studies in P. patens along with comparative studies that seek to identify cell wall character-
istics that correlate with adaptation to diverse habitats can enhance our understanding of cell wall biosynthesis and land plant evolution by elucidating the relationships among glycosyl transferase functional diversification, cell wall structural and bio-
chemical specialization, and the roles of cell wall properties in plant adaptation.

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