INTRODUCTION

The primary cell wall (PCW) has many essential biological roles, including tissue cohesion, defence (e.g. against microbes), ion exchange, the production of oligosaccharins and the regulation of cell expansion (Goldberg et al., 1994; Brett and Waldron, 1996; Cassab, 1998; Dumville and Fry, 1999; Fry, 1999). Demands on the PCW, and therefore its optimal composition, may have changed during periods of rapid plant evolution. In particular, colonization of the land by the first bryophytes is likely to have exposed these plants to novel ecological problems, the solution to which may have driven rapid evolution of the PCW.

Few studies have been undertaken of cell wall composition in non-vascular land plants (Chodat and Cortesi, 1939; Edelmann et al., 1998). Among bryophytes, liverworts broadly resemble gymnosperms in their PCW sugar residue composition, the major neutral monosaccharide residues being Glc > Gal > Man > Xyl = Ara > Fuc = Rha (Thomas, 1977; Thomas et al., 1984). However, there is no information on the nature of the polysaccharides that contain these sugar residues in bryophytes. Even the sugar residue composition is not fully defined: for example, most studies do not report which acidic sugars are present in bryophytes (Thomas, 1977). Das and Rao (1966b) reported the presence of mannanuronic acid (ManA) in cell walls of the liverwort Riccardia. However, this report of ManA in liverwort cell walls is unusual as GalA > GlcA > 4-O-methyl-GlcA are the most commonly occurring acidic sugars in angiosperm cell walls. Galactoglucomannans that have a structure similar to those occurring in angiosperms and gymnosperms have been characterized from an aquatic moss (Geddes and Wilkie, 1971).

Variation exists in cell wall composition between different algal taxa and is widely used in algal classifications (Stace, 1981). On the basis of morphological and biochemical evidence, there is now wide support for the closest extant ancestor of land plants being amongst the charophycean green algae (Manhart and Palmer, 1990; Kranz et al., 1995). Although the charophycean green algae Chara and Nitella have been widely used as models for studies of plant cell growth, their PCW composition has not been well studied. Indeed, both Chara and Nitella differ from land plants in lacking detectable hydroxyproline—a component of the major PCW glycoproteins, extensins (Gotteli and Cleland, 1968; Kieliszewski and Lamport, 1994).

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In this paper the evolution of the primary cell wall in land plants is documented. The polysaccharide composition of a variety of charophycean green algae and bryophytes is reported. Comparisons are drawn with results obtained from vascular land plants.

**MATERIALS AND METHODS**

**Source of plant material**

Sources of non-vascular botanical material are listed in Table 1. Details of lycopodiophyte and fern material are listed in Popper et al. (2001). Young leaf tissue of Flagellaria guineensis Schum. was obtained from the Royal Botanic Garden Edinburgh (Accession number 19720171). Seeds of Secale cereale L., Triticum aestivum L., Zea mays L. and Hordeum vulgare L. were obtained commercially, grown in the dark, and alcohol-insoluble residue (AIR) was prepared from the coleoptiles.

**Preparation of alcohol-insoluble residue**

Preparation of alcohol-insoluble residue was as described by Popper et al. (2001).

**Paper chromatography (PC) and thin-layer chromatography (TLC)**

Whatman No. 1 paper was used for analytical PC. One-dimensional PC was by the descending method, whereas 2-dimensional PC used the ascending method. Solvent systems used were: (1) butan-1-ol : acetic acid : water (12 : 3 : 5 by volume); (2) as for system 1 for 16 h followed, in the same dimension, by ethyl acetate : pyridine : water (8 : 2 : 1 by volume) for 18 h; (3) as for system 1 for 12 h followed, perpendicular to the first dimension, by phenol : water (4 : 1 w/w); and (4) ethyl acetate : pyridine : water (8 : 2 : 1 by volume) for 42 h. Paper chromatograms were stained with aniline hydrogen-phthalate; faint spots were more readily visible by their fluorescence when viewed under a 366-nm UV lamp (Fry, 2000). TLC was on Merck silica gel (VWR International, Poole, UK). The solvent system used was either (5) butanol : acetic acid : water (3 : 1 : 1 by volume), or (6) butanol : acetic acid : water (2 : 1 : 1 by volume). TLC plates were stained with thymol–sulfuric acid (Jork et al., 1994).

**Paper electrophoresis (PE)**

PE was on Whatman No. 1 paper. Samples were loaded 12 cm from the cathode end. The paper was wetted with...
buffer (acetic acid : pyridine : water; 10 : 1 : 378 by volume), blotted to remove excess and run with pH 3.5 buffer (acetic acid : pyridine : water; 10 : 1 : 189 by volume). Typical running conditions for paper of width 38 cm were 3-0 kV, 100 mA for 1·5 h. Electrophoretograms with radioactive markers were autoradiographed prior to staining with aniline hydrogen-phthalate.

**High-pressure liquid chromatography (HPLC)**

A Dionex HPLC (Camberley, UK) was used with a CarboPac PA1 anion-exchange column (4 mm internal diameter, 250 mm long) and a pulsed amperometric detector. The flow rate was 1·0 ml min⁻¹ at room temperature, and 20 μl samples in H₂O were injected. Before injection, samples were filtered (Millipore, Bedford, MA, USA). The separation method followed Gibeaut and Carpita (1993).

**Ion-exchange chromatography**

Prior to ion exchange, samples were de-lactonized by adjusting to pH 13 using 0·1 M NaOH and incubating for 8 s. Samples were neutralized with 0·1 m formic acid and made up to 1 ml before loading onto columns (1·5 ml bed volume) of Dowex 1 × 4–200 strongly basic anion exchanger in the chloride form (Sigma, Poole, UK). The resin was pre-treated by washing (1 h each wash) in (a) 0·5 M NaOH; (b) twice in 0·5 M formic acid; and (c) in 2 M sodium formate. The resin was finally washed in buffer A (10 mM pyridinium formate, pH 5·5). Neutral sugars were eluted with 4 ml buffer A. The acidic fraction was then eluted with 4 ml buffer B (pyridine : formic acid : water; 1 : 1 : 23, pH 5·5). Neutral and acidic fractions were dried, re-dissolved in 100 μl water and the neutral fraction was de-salted using cation-exchange resin. Neutral sugars and sugar acids were dried, re-dissolved in 50 μl water and the solution was then separated into neutral and acidic products. Neutral sugars were analysed by PC (solvent systems 1 and 2), TLC (solvent system 5) and HPLC.

**Cellulose digestion**

Hemicellulose extracted from 0·1 g AIR was dissolved in 1 ml 50 mM acetate buffer, Na⁺, pH 4·7. Cellulase (2·5 units; E.C. 3.2.1.4 isolated from Trichoderma longibrachium; Megazyme) was added and the mixture incubated at 20 °C for 2 d before analysis by TLC.

**Xyloglucan-specific endoglucanase (XEG) digestion**

One milligram AIR was incubated for 5 min in 0·5 ml 50 mM acetate, Na⁺, pH 3·0 containing 0·1 % XEG (E.C. 3.2.1.4 isolated from Aspergillus aculeatus; Novo Nordisk, Bagsvaerd, Denmark; Pauly et al., 1999). The products were analysed by silica gel TLC (solvent systems 5 and 6).

**Acid hydrolysis**

Each AIR sample (20 mg) was subjected to hydrolysis in 1 ml 2 M TFA at 120 °C for 1 h. The hydrolysate was then dried in vacuo and re-dissolved in 50 μl water. The hydrolysate was either subjected to 2-dimensional PC or separated into neutral sugars and sugar acids by ion exchange. Neutral sugars were analysed by PC (solvent systems 1, 2 and 3), and the sugar acids by PE.

**RESULTS**

**Mixed-linkage glucan**

In an investigation of the taxonomic distribution of MLG, licheninase digests of PCWs of a variety of plants were analysed by TLC and HPLC. MLG was clearly detected in rye, maize, barley, wheat and Flaggellaria guineensis, confirming the suitability of the methods used. MLG was undetectable in PCW-rich material derived from the charophytes Chara corallina and Coleochaete scutata. In all but one of the bryophytes tested, MLG was undetectable (Fig. 1; Table 2). The exception was the leafy liverwort Lophocolea bidentata, in which licheninase digestion yielded a range of oligosaccharides. The major oligosaccharides [degree of polymerization (DP) approx. 2–6] were purified by gel-permeation chromatography on Bio-Gel P-2 (Bio-Rad, Hemel Hempstead, UK); acid hydrolysis of these yielded Glc and Ara, showing that these oligosaccharides...
differed from those of barley MLG, which contained only Glc (Woodward et al., 1983). However, the licheninase-digestible polysaccharide in *L. bidentata* was not always detectable, being clearly visible in only five out of seven replicates of *L. bidentata* collected in May, and undetectable in four replicates collected in July.

Licheninase was also able to digest polysaccharides from the chlorophyte *Ulva lactuca* to products that differed from those typically produced on digestion of MLG from gramineous monocotyledons in having a higher DP and containing xylose as well as glucose (data not shown). The reducing terminus of these oligosaccharides was glucose, as shown by production of [3H]glucitol upon reaction with NaB₃H₄ (data not shown).

**Xyloglucan**

Driselase digestion yields the disaccharide isoprimeverose from xyloglucan but from no other known polymer. PC and HPLC of the Driselase digests of PCW-rich material from a variety of land plants showed isoprimeverose to be an appreciable component in all the land plants tested, including bryophytes (Table 2). However, isoprimeverose was not detectable in Driselase digests of PCW-rich material derived from the charophyte *Chara* (Figs 2 and 3). If exogenous xyloglucan was added to *Chara* AIR prior to Driselase digestion, isoprimeverose was detectable among the products. The limits of detection were 0.01 % xyloglucan (w/w, xyloglucan : AIR) by PC (Fig. 2) and 0.02 % (w/w, xyloglucan : AIR) by HPLC (Fig. 3). Some monosaccharides are released from *Chara* by pre-treatment with 0.1 m TFA; they can be clearly seen in the non-digested *Chara* sample.

Sequential pectic and hemicellulosic extracts of *Chara* PCW-rich material also yielded no isoprimeverose on Driselase digestion (results not shown). Driselase digestion of *Coleochaete* AIR also did not result in the production of isoprimeverose in a quantity detectable by our methods (limit of detection approx. 0.01 % w/w; results not shown).

Although cellulase digested *Chara*, none of the digestion products corresponded to the xyloglucan oligosaccharides (e.g. XXXG, XXFG, XLLG, XFFG; Fry et al., 1993) typically produced by cellulase digestion of xyloglucans from dicotyledons. The cellulase digestion products of *Chara* AIR appeared to correspond to oligosaccharides of xylan, which is also partially digested by cellulase (TLC results not shown). XEG, a specific xyloglucanase, did not digest any of the polysaccharide fractions sequentially extracted from *Chara* (Fig. 4A). Additionally, XEG did not digest AIR from *Klebsormidium* (Fig. 4B) or *Nitella* (M. Pauly, Max Planck Institut für Pflanzenphysiologie, Golm, Germany, pers. comm.). XEG digested bryophyte AIR to yield low concentrations of the xyloglucan-derived oligosaccharide XXXG (TLC results not shown).

TFA hydrolysis of *Coleochaete* and *Klebsormidium* AIRs showed that they each had approximately equimolar xylose and glucose residues. Since xyloglucan was undetectable, this Xyl probably arose from β-xylans. Very little xylose, a
Table 2. Polysaccharide and monosaccharide content of plant taxa

<table>
<thead>
<tr>
<th>Classification</th>
<th>Species</th>
<th>MLG</th>
<th>Xyloglucan</th>
<th>GalA</th>
<th>GlcA</th>
<th>αGlcA-(1→3)-Gal</th>
<th>Mannose</th>
<th>3-O-Methylrhamnose</th>
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</table>

-, Not detectable; ±, trace; +, present at low concentration; ++, present at moderate concentration; ++++, present at high concentration; blank cell, not tested.

* Licheninase-digestible polysaccharide present (in the case of Lophocolea not always detectable; see text), but not simple MLG.

† 3-O-methylrhamnose was present in homosporous lycopodiophytes but absent from homosporous lycopodiophytes.
major component of xyloglucan, was released on TFA hydrolysis of Coleochaete AIR; again, this is compatible with the absence of xyloglucan. According to all the above criteria, xyloglucan appears to be absent from charophycean green algae.

Uronic acids

In the PCW, uronic acid residues are found as constituents of xylans, pectins, glucuronomannans and arabinogalactan-proteins. The acidic fraction of TFA hydrolysates from a variety of land plants was analysed by PE. GalA was found to be the major uronic acid in all the bryophytes and charophycean green algae tested (Table 2; Fig. 5). The concentration of GalA was higher in the charophycean green algae and bryophytes than in any of the vascular plants (Table 3). Additionally, GlcA was found in high concentration in the two charophytes tested (Chara and Coleochaete), leafy and thalloid liverworts, and Sphagnum (one of the most basal moss genera) (Fig. 5 and similar results, not shown). GlcA was not present in high concentration in any of the more recently evolved moss lineages or in vascular plants.
Mannuronic acid has been reported as the major uronic acid residue in the PCWs of the leafy liverwort *Riccardia* (Das and Rao, 1963, 1966a, b). However, our methods did not detect ManA in any land plants, including liverworts. Both GlcA and GalA residues were clearly detected in the cell walls of all liverworts tested, both thalloid and leafy, as well as in the hornwort *Anthoceros*. Das and Rao (1963, 1966) did not report the presence of either GlcA or GalA in the cell walls of *Riccardia*, but reported that the *R*F values (mobility of compound relative to that of the solvent front) of GlcA and ManA on PC in ethyl acetate : pyridine : acetic acid : water (5 : 5 : 1 : 3) only differed slightly. Therefore, it is possible that ManA is not present in liverwort cell walls and that Das and Rao (1966a, b) mistook either GlcA or GalA for ManA.

By our method of separation (PE), 4-O-methylglucuronic acid (4-O-Me-GlcA) is only just distinguishable from GlcA. We found that 4-O-Me-GlcA was either undetectable or indistinguishable from GlcA in any of the land plants analysed. 4-O-Me-GlcA is known from xylem (secondary cell walls) and may be present at much lower concentrations in primary cell walls. Darvill et al. (1980) reported that in suspension-cultured sycamore cells, 4-O-Me-GlcA constitutes approx. 0.25 % of the monosaccharide residues present in the wall (on a dry weight basis). This correlates with the results of Harris et al. (1997), who reported that the unlignified cell walls of dicotyledons and non-gramineous monocotyledons contain 0.3–0.8 % 4-O-Me-GlcA w/w of the cell wall.

TFA hydrolysis of AIR from *Anthoceros* gave large amounts of an acidic disaccharide (Fig. 6). This product was purified by chromatographic methods and has recently been identified as α-GlcA-(1→3)-Gal by N.M.R. (I. H. Sadler, pers. comm.). It appears to be confined to *Anthoceros*.

**3-O-Methylrhamnose**

3-O-Methylrhamnose (Table 2; Fig. 6) has not previously been reported from charophytes, bryophytes or homosporous lycopodiophytes. We have purified this unusual sugar from acid hydrolysates of the AIR of the hornwort *Anthoceros* by PC and characterized it by NMR (data not shown; collaboration with I. H. Sadler, Department of Chemistry, The University of Edinburgh, UK). We found it to occur in the cell walls of charophytes, bryophytes and homosporous lycopodiophytes (Table 2).

**Mannans**

In the PCW, mannose residues are present in mannan, glucomannans, galactoglucomannans and glucuronomannans, with lower concentrations of mannose residues present in many wall enzymes such as peroxidases. In an investigation of the distribution and relative quantity of mannose residues present in many wall enzymes such as peroxidases. In an investigation of the distribution and relative quantity of mannose residues present in many wall enzymes such as peroxidases. In an investigation of the distribution and relative quantity of mannose residues present in many wall enzymes such as peroxidases.
This is the first detailed study of the cell wall compositions of bryophytes in comparison with those of their charophycean ancestors and vascular successors. Cell walls of charophycean green algae, a hornwort, thalloid and leafy liverworts, and primitive mosses were found to contain high concentrations of GlcA and GalA residues. In contrast, walls of the more advanced (and more drought-tolerant) mosses have a much lower concentration of GlcA. Additionally, a novel disaccharide is described from hornwort cell walls. The PCW polysaccharide xyloglucan was found to be present in all land plants but is lacking from the PCWs of charophycean green algae. Mannose was found to be present in high concentration in the PCWs of liverworts, mosses and lycopodiophytes, and present at low concentration in the PCWs of charophytes and euphyllophytes (= all vascular plants other than lycopodiophytes; Kenrick and Crane, 1997).

**TABLE 3. Summary of the major trends in polysaccharide composition of plant taxa**

<table>
<thead>
<tr>
<th>Group</th>
<th>Isoprimeverose</th>
<th>GalA</th>
<th>GlcA</th>
<th>αGlcA-(1→3)-Gal</th>
<th>Man</th>
<th>3-O-MeGal</th>
<th>3-O-MeRha</th>
</tr>
</thead>
<tbody>
<tr>
<td>Charophytes</td>
<td>−</td>
<td>++</td>
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<td>Hornwort</td>
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<td>Liverworts &amp; Sphagnum</td>
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<td>Advanced mosses</td>
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<td>Homosporous lycopodiophytes</td>
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<td>Heterosporous lycopodiophytes</td>
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−, not detectable; ±, trace; +, present at low concentration; ++, present at moderate concentration; ++++, present at high concentration.

**DISCUSSION**

Fig. 5. Paper electrophoresis (PE) of the acidic fraction of acid hydrolysates of bryophyte AIRs. Samples were run by PE at pH 3.5 and 3.0 kV for 1.5 h. An internal marker of [¹⁴C]GalA (trace; not detectable by staining) was added to each hydrolysate (a–f) before loading onto the PE. A, PE stained with silver nitrate; B, autoradiogram of PE. Hydrolysates were from (a) *Lophocolea bidentata*, (b) *Anthoceros caucasicus*, (c) *Sphagnum palustre*, (d) *Dicranum scoparium*, (e) *Plagiothecium undulatum* and (f) *Mnium hornum*. Markers were (g) GalA + iduronic acid (IdA) + GlcA and (h) MannA + guluronic acid (GulA).
The results indicate that major changes in PCW composition accompanied major evolutionary steps (Table 3). In particular, there are quantitative and qualitative differences between the charophytes and the bryophytes, and between those bryophytes thought to be primitive and those thought to be more advanced (Bopp and Capesius, 1996; Hedderson et al., 1996). This supports Stebbins’ hypothesis (1992) that alterations in
cell wall composition may have been associated with bryophyte diversification.

The first land plants are thought to have resembled extant bryophytes (Mishler et al., 1994). Hornworts and liverworts cling to the moist substrata on which they grow, and some primitive mosses grow submerged in water. In the absence of specialized conducting tissues, height is physiologically limited by the time it takes water to diffuse between cells and reach aerial portions of the plant. The time for water to diffuse through a string of cells end on end is relatively long (Nobel, 1983). Therefore, some kind of conducting tissue is a physiological necessity for the continued vertical growth of land plants. Increased vertical growth increases competitiveness and survival by allowing greater access to light. The water-conducting tissue, hydrom, of advanced mosses, and the apparently homologous xylem of vascular plants (Scheier, 1980; Mishler and Churchill, 1984, 1985; Mishler et al., 1994) solve this problem in these plants; and the problem does not arise with aquatic charophytes. However, primitive bryophytes may require unique sponge-like properties of their PCW to permit the efficient distribution of water between all the parenchymatous cells of their aerial tissues. Thus, the characteristic features of lower bryophytes (high GalA, GlcA and Man) may be connected with this requirement. One of the major differences observed between primitive bryophytes (hornworts, liverworts and the moss genus Sphagnum) and more advanced bryophytes (all other moss genera investigated) was the high concentration of GlcA in primitive bryophytes; GlcA was present at very low concentration in more advanced bryophytes and all other land plants investigated.

The shared presence of high GlcA concentration in charophytes and primitive bryophytes is notable as GlcA was present at very low concentration in all other land plants investigated. GalA was also present at higher concentrations in charophytes and bryophytes than in vascular plants. Both these observations support molecular and morphological evidence that suggests that bryophytes (and ultimately all land plants) evolved from a common ancestor within the charophytes (Pickett-Heaps, 1976; Mattox and Stewart, 1984; Graham, 1993).

However, we found xyloglucan to be absent from the charophytes Chara, Coleochaete and Klebsormidium, although present in all land plants investigated. This conclusion conflicts with previous reports suggesting that xyloglucan is present in the charophycean cell wall. Anderson and King (1961) reported that Chara has a cell wall composition similar to that of land plants. This comparison was based on the relative concentrations of the main classes of cell wall polymers (hemicellulose, pectic polysaccharides and cellulose) present in Chara and a variety of land plants. However, the hemicellulose fraction was not characterized and the presence of hemicellulose does not prove the existence of xyloglucan. Morrison et al. (1993) reported that the 1 M KOH extract of Nitella contained xyloglucan. The extracted polysaccharide was reported to be composed of 10 % Fuc, 21.7 % Xyl, 10.4 % Gal and 45.8 % Glc residues w/w (Morrison et al., 1993). Xyloglucan from dicotyledons has a similar monosaccharide composition. However, methylation analysis revealed that all the Xyl in the Nitella polysaccharide was 2- and/or 4-linked Xyl. If xyloglucan with a similar structure to that in angiosperm cell walls had been present, terminal Xyl would have also been present. Therefore, the results of Morrison et al. (1993) do not conclusively show the presence of xyloglucan in Nitella cell walls; many of the sugar linkages reported could result from the presence of other hemicelluloses such as xylans (4-linked Xyl) and possible contamination with starch (4- and 4,6-linked Glc). Acid hydrolysis of Coleochaete AIR yielded a very low concentration of xylose residues, confirming that xyloglucan could not have been a major component.

All land plants ultimately descend from a common algal ancestor from which the modern Charophyceae are also descended (Pickett-Heaps, 1976; Mattox and Stewart, 1984; Graham, 1993). It is possible that charophycean green algae have indigestible xyloglucan with no unsubstituted Glc. Such xyloglucan would fail to yield isopimperoneose upon Driselase digestion or oligosaccharides upon cellulase or XEG digestion. However, Morrison et al. (1993) reported the presence of 4-linked Glc in Nitella hemicellulose, and xyloglucan with 4-linked Glc residues would be expected to be digestible by any of the three enzymes used in this study.

Driselase digestion yields only a low concentration of isopimperoneose from bryophyte AIR. Therefore, xyloglucan is likely to be present in bryophyte PCW at a much lower concentration than is typically found in the angiosperm PCW. However, it is possible that xyloglucan in the bryophyte PCW may have reduced digestibility, either because of the structure of the polymer itself, or because of the structure and composition of the PCW. Additionally, XEG digestion of bryophyte AIR yielded only a low concentration of the xyloglucan-derived oligosaccharide XXXG. Bryophyte xyloglucan therefore appears to differ from typical angiosperm xyloglucan both in concentration and structure. It is possible that the bryophytes do not have all the enzymes required to make typical angiosperm xyloglucan.

Glucomannans have been found as a major hemicellulose component in the secondary cell walls of the gymnosperms (10 % total cell wall w/w) and a minor hemicellulose component in the secondary cell walls of dicotyledons (3–5 % total cell wall w/w) (Matheson, 1990). They have been reported to constitute approx. 15 % of the total secondary cell walls of a fern, Pteridium aquilinum (Bremer and Wilkie, 1971). Our results show that the PCWs of leptosporangiate ferns, gymnosperms and angiosperms contained far less mannose than those of the bryophytes, lycophydiophytes, equisetophytes and psilophytes. It is possible that the PCW composition of the bryophytes, lycophydiophytes, equisetophytes and psilophytes is similar to that of the secondary cell wall of leptosporangiate ferns, gymnosperms and angiosperms.

The unusual disaccharide repeat unit α-GlcA-(1→3)-Gal from Anthoceros (hornwort) AIR has been characterized. Hornworts are thought to be the most primitive land plants (Renzaglia et al., 2000). The occurrence of the unusual disaccharide repeat unit α-GlcA-(1→3)-Gal in Anthoceros, and its absence from all other land plants investigated, may suggest that the polysaccharide containing the disaccharide
repeat unit was not essential to land plant survival. The disaccharide repeat unit may be associated with mucilage rather than PCW, and potentially may be a way in which algae growing in areas that dry out seasonally, and primitive land plants, prevent desiccation. The high concentration of uronic acid in the mucilage or PCW could potentially increase water retention.

3-0-Methylrhamnose (trivial name acofrlose) was detected in the PCWs of charophytes, bryophytes and homosporous lycopodiophytes. Best known from bacteria (Williams and Wnder, 1980), this sugar has been reported from polymers of the fern Osmunda (Akiyama et al., 1988), as a component of an acidic polysaccharide in the green alga Chlorella (Ogawa et al., 1997), and in resin exudates from gymnosperms (Anderson and Munro, 1969). 3-O-Methylrhamnose is present in the PCWs of charophytes, their closest immediate descendants, the bryophytes, and homosporous lycopodiophytes. It seems likely that many different plant taxa, excluding the angiosperms, have the ability to synthesize 3-O-methylrhamnose. However, most taxa synthesize low concentrations of 3-O-methylrhamnose or have lost the pathway for methylation of rhamnose as it does not appear to be necessary for land plant survival. The existence of 3-O-methylrhamnose 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).

In conclusion, primary cell wall composition has been found to differ between monophyletic groups of plants (supported by morphological and molecular data). It is likely that during the emergence of these groups, plants were subjected to particularly rigorous selection pressures. The emergence of these groups is also linked with fundamental changes in plant habitat e.g. the aquatic-to-land transition, and with the acquisition of vascular tissue and upright habit. Variation in cell wall composition may be related to ecological pressures experienced during evolution. In particular, the presence of xyloglucan in all land plants and its absence from all charophytes investigated suggests that the acquisition of xyloglucan may have been a pre-adaptive advantage for the colonisation of land.

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LITERATURE CITED


